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ORIGINAL ARTICLE

Scale-dependent spatial population dynamics of gall-makers on oak

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Abstract

The patterns of synchrony in the population fluctuations of six species of gall-makers on oak (Hymenoptera, Cynipidae and Diptera, Cecidomyiidae) were analyzed over a small-scale transect (8 km) and a large-scale transect (500 km). Gall-maker species differed in their degree of synchrony. At the small scale some species showed synchrony among local sites, whereas at the large scale, with one exception, population fluctuations of all species were largely independent. The patterns of synchrony differed between the two spatial scales. At the small scale a considerable degree of synchrony was found among sites for two species, *Cynips divisa* and *Neuroterus quercusbaccarum*, whereas at the large scale no synchrony was seen for these species. For one species, *Macrodiplosis volvens*, the fluctuations were asynchronous at both the small and large scales. At the large scale, synchrony among sites was found for one species: the fluctuations of *Neuroterus anthracinus* were largely synchronous at both scales (i.e. over several hundred kilometers). Distance-dependent synchronies (i.e. decreasing synchrony with increasing distance) were found for only one species, *Neuroterus anthracinus*. In summary, the levels of synchrony in the population fluctuations of these insects differed among species and were scale-dependent. Scaling up from the small scale to the large scale does not seem appropriate.

Key words: Cecidomyiidae, Cynipidae, gall-makers, population dynamics, *Quercus*, spatial scale, synchrony.

INTRODUCTION

The densities of insects fluctuate over time and the analysis of such fluctuations is a major field of entomological research (e.g. Cappuccino & Price 1995; Huffaker *et al.* 1999). Comparative analysis of a number of spatially arranged populations can be used to evaluate the degree of synchrony among populations with respect to population fluctuations (e.g. Hanski & Woiwod 1993; Sutcliffe *et al.* 1996). Two main questions are posed in the investigation of such spatial population dynamics (see Liebhold & Kamata 2000): (i) which patterns of synchrony (synchrony or asynchrony) are exhibited between populations distributed over space; and (ii) how do these patterns of synchrony arise? Analysis of spatial population dynamics is fundamental for the understanding of population dynamic processes such as metapopulation dynamics and outbreaks of pests on larger scales (e.g. McCullough 2000). For pest species, predictions of whether outbreaks will be spatially correlated over larger areas would be valuable data to inform management.

Three processes that may lead to synchrony have been identified: external factors (e.g. climate), dispersal between populations, and biological interactions (e.g. predation) (Bjørnstad *et al.* 1999; Ranta *et al.* 1999; Kendall *et al.* 2000; Lundberg *et al.* 2000). It appears likely that these processes act at different scales. In fact, studies have provided examples of scale-dependent spatial synchrony (Sutcliffe *et al.* 1996; Haydon & Steen 1997; Bowman *et al.* 2000; Paradis *et al.* 2000). At larger scales, for instance, weather factors may be the

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dominant synchronizing factor, whereas at smaller scales dispersal between populations may be more important (Hanski & Woiwod 1993; Steen *et al.* 1996; Sutcliffe *et al.* 1996).

Most studies on insects at a small scale (regarding processes over distances of up to a few kilometers) have found high degrees of synchrony (e.g. Thomas 1991; Hanski & Woiwod 1993; Sutcliffe *et al.* 1996). However, there are some instances where asynchronous dynamics have been documented (Kindvall 1996; Ranius 2001; Biedermann 2005). The degree of synchrony among population fluctuations has been shown to be dependent on the distance between populations (e.g. Hanski & Woiwod 1993; Sutcliffe *et al.* 1996; but see Kindvall 1996), with the degree of synchrony between populations decreasing with increasing distance. However, for insects there is a general shortage of empiric studies that have analyzed population synchrony at different spatial scales (but see Pollard 1991). In particular, studies at large scales (regarding processes exceeding distances of hundreds of kilometers) have been rarely attempted (Hanski & Woiwod 1993; Sutcliffe *et al.* 1996), apart from outbreak species (McCullough 2000; Williams & Liebhold 2000).

The aim of this study was to investigate the scale-dependent spatial patterns of the population dynamics of gall-makers on oak (Hymenoptera, Cynipidae and Diptera, Cecidomyiidae). Gall-makers provide an ideal study system for the analysis of population dynamics at large scales, because a large number of accurate population estimates can be relatively easily obtained for these species by simply counting the number of galls, owing to the sessile nature of the galls on plants. The population density of the gall-makers was monitored simultaneously for four years at two spatial scales: a small scale and a large scale. The following questions were addressed:

1. Do the patterns of synchrony differ at the small and large scale?
2. Does the degree of synchrony decrease with distance between populations?
3. Are there differences in the patterns of synchrony among the gall-maker species?

MATERIALS AND METHODS

Sampling

To monitor the population dynamics of gall-makers on oak leaves (*Quercus robur*, *Quercus petraea*), the density of gall-makers was estimated in September. At this time the galls of all species can be found simultaneously on leaves. In bivoltine gall wasps the asexual (agamic) generation is present (except in *Andricus curvator*, for which the sexual generation occurs on leaves); in univoltine gall midges there is only one generation per year. At each sampling location 25 leaves of four individual oak trees (where available) were collected. In a preliminary test in which a range of numbers of leaves were tested, 25 leaves was found to be sufficient to provide a stable moving average as an estimate of gall density. The leaves were randomly selected at heights of about 1.5–2 m, irrespective of tree height. For the gall wasp *Neuroterus quercusbaccarum*, the density of galls is reportedly similar throughout the entire canopy of oak trees (Kampichler & Teschner 2002). Consequently, it can be assumed that samples taken at a height of 1.5–2 m represent the density of the entire tree. The identity and number of galls was determined in the laboratory using the keys of Buhr (1965) and Redfern and Askew (1992).

From 1999 to 2002 the spatial population dynamics of the gall-makers on oak leaves was analyzed at two spatial scales. Small-scale population dynamics were studied in a transect of approximately 8 km in length comprising seven sites with areas of approximately 1 km × 1 km (see Fig. 1b). At each site there were 7–12 randomly distributed sampling locations (each representing 25 leaves, see above), and the mean density at each of the seven sites was calculated. The transect was situated in northern Germany, 6 km south of the city of Oldenburg.

Large-scale population dynamics were studied on a transect across Germany. Ten sites (see Fig. 1a) with areas of approximately 2 km × 2 km were chosen over approximately 500 km. At each site there were 7–12 randomly distributed sampling locations (each representing 25 leaves, see above) and the mean density at each of the ten sites was calculated.

Statistical analysis

The degree of synchrony between the sites was measured using an approach that is based on counting correlated changes in the direction of two time series (details see Buonaccorsi *et al.* 2001). The degree of synchrony, τ_{ij} (ranging from –1 to 1), between two time series *i* and *j* was calculated as follows:

$$\tau_{ij} = 2A_{ij} - 1 \tag{1}$$

with $A_{ij} = s_{ij}/(T - 1)$, where s_{ij} is the number of times the two series *i* and *j* have the same direction of change (increase or decrease) and *T* is the length of the time series. A value of $\tau_{ij} = 1$ indicates that all changes of the

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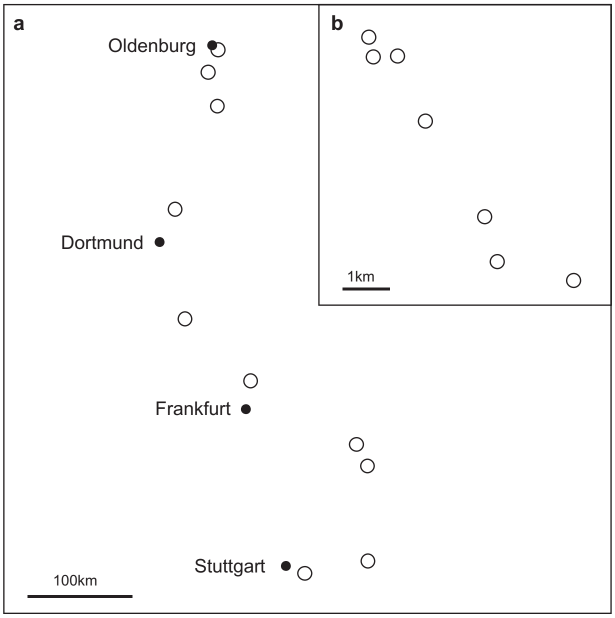

Figure 1 Maps of (a) the large-scale transect (throughout Germany) and (b) the small-scale transect (situated 6 km south of the city of Oldenburg) established to analyze the spatial population dynamics of gall-makers on oak. The circles represent sampling sites (each consisting of 7–12 sampling locations).

two time series are in the same direction, whereas a value of $\tau_{ij} = -1$ means that all changes are in the opposite direction. A value of $\tau_{ij} = 0$ occurs when there is an equal number of changes in the same direction as there are in the opposite direction. The 95% confidence intervals were calculated as suggested by Buonaccorsi *et al.* (2001) and Bjørnstad *et al.* (1999): the data were re-sampled with replacement, and each bootstrap sample is a sample as large as the observed sample. The bootstrapping was repeated 1000 times. The upper and lower 95% confidence intervals were calculated using percentiles. A possible distance-dependency of synchrony between sites was tested by Mantel tests using zt software (Bonnet & Van de Peer 2002). The Mantel tests were applied to two matrices, the geographic distance between sites and the synchrony, τ, between sites.

RESULTS

For the two transects over the 4 years, a total of 14 species of leaf gall-makers were detected on oak leaves, including 12 species of gall wasps and two species of gall midges. Further analyses were confined to six species, because for some species, *Andricus curvator* Hartig, 1840, *Andricus quadrilineatus* Hartig, 1840, *Cynips disticha* Hartig, 1840, *Cynips longiventris* Hartig, 1840, *Cynips quercusfolii* (L., 1758), and *Trigonaspis megaptera* (Panzer, 1801), their distribution was too restricted or their density was too low for sound statistics. For two species, determination to species level was not possible for all specimens (galls of *Neuroterus albipes* (Schenk, 1863) and *Neuroterus tricolor* (Hartig, 1841) can easily be confused without rearing the gall-making larvae to adults).

At the small scale, a considerable degree of synchrony was found among sites for three species, *Cynips divisa* Hartig, 1840, *Neuroterus anthracinus* (Curtis, 1838), and *Neuroterus quercusbaccarum* (L., 1758), (Table 1). For the other three species, *Macrodiplosis dryobia* (F. Löw, 1877), *Macrodiplosis volvens* Kieffer, 1895, and *Neuroterus numismalis* (Geoffroy in Fourcroy, 1758), the densities did not fluctuate synchronously. For two species, *Macrodiplosis dryobia* and *Neuroterus quercusbaccarum*, the degree of synchrony decreased significantly with increasing distance (Table 2).

At the large scale, only in one species was a high degree of synchrony detected (Table 1). The population dynamics of *N. anthracinus* was largely synchronous over several hundred kilometers, but the degree of synchrony decreased significantly with increasing distance (Table 2). For two species, *M. dryobia* and *N. numismalis*, a considerable degree of synchrony existed. In all other species no synchrony was found. Further, in all species except *N. anthracinus*, the degree of synchrony was not distance-dependent.

DISCUSSION

The results presented here are interesting because there are very few studies that have compared the degrees of synchrony of a number insect species in one particular system at more than one spatial scale. Although this study has some temporal limitations in that the population dynamics of gall-makers were documented for only 4 years, marked differences in the levels of synchrony were found. The observed patterns of synchrony varied broadly among species, even for species with very similar life-histories, such as the two gall midges *M. dryobia* and *M. volvens*. For some species the levels of synchrony differed between the small and the large scale. For *C. divisa* and *N. quercusbaccarum*, a considerable degree of synchrony at the small scale contrasted with more or less asynchronous dynamics at the large scale. In these species the synchrony reduced as distance

Table 1 Mean levels of synchrony of six gall-makers on oak at two spatial scales

	Small scale		Large scale	
Species	Mean synchrony (τ)	Confidence interval (95%)	Mean synchrony (τ)	Confidence interval (95%)
Cynips divisa	0.27	0.14, 0.68	–0.14	–0.32, 0.29
Macrodiplosis dryobia	–0.05	–0.21, 0.43	0.23	0.05, 0.61
Macrodiplosis volvens	–0.02	–0.14, 0.68	–0.20	–0.29, 0.19
Neuroterus anthracinus	0.81	0.62, 1.00	0.69	0.63, 0.87
Neuroterus numismalis	–0.02	–0.02, 0.37	0.20	0.07, 0.51
Neuroterus quercusbaccarum	0.37	0.17, 0.81	0.04	–0.04, 0.33

Table 2 Results of Mantel tests measuring the correlation between distance and synchrony at two spatial scales

	Small scale		Large scale	
Species	r	*P*	r	*P*
Cynips divisa	–0.004	0.500	0.09	0.291
Macrodiplosis dryobia	–0.61	0.002	–0.05	0.408
Macrodiplosis volvens	0.26	0.138	0.21	0.093
Neuroterus anthracinus	0.09	0.351	–0.47	0.004
Neuroterus numismalis	0.24	0.142	0.12	0.237
Neuroterus quercusbaccarum	–0.45	0.018	–0.20	0.092

increased, and no synchrony was present at the large scale. Except for one species, the observed population synchrony of the oak gall-makers was not distance-dependent, at either the small or the large scale. This contrasts with the findings from most other studies on insects, in which population synchrony was found to decrease with increasing distance. For example, Sutcliffe *et al*. (1996) tested for distance-dependent synchrony in butterflies at scales of up to a few kilometers. They found a decrease in synchrony with increasing distance in 73% of 215 species/site combinations (of 21 species and 56 transects). Raimondo *et al*. (2004) also reported high levels of synchrony for ten forest Lepidoptera at a large scale and distance-dependency in most species.

From these observations the question arises of what the causes of the synchrony patterns in gall-makers are. *Neuroterus anthracinus* was the only species in the present study showing high levels of synchrony. When the life-history traits of *Neuroterus anthracinus* are compared with those of the two other *Neuroterus* gall wasps (Buhr 1965), two traits could be related to the differences in synchrony. First, the sexual generation of *N. anthracinus* does not occur on oak leaves but on buds. However, the relevance of this explanation of the synchrony pattern remains unclear. Second, the agamic generation of *N. anthracinus* overwinters as adults, which emerge in October. This is in contrast to *Neuroterus numismalis* and *Neuroterus quercusbaccarum*, which overwinter in the larval stage within galls. It seems plausible that the overwintering adults of *N. anthracinus* would be more exposed to harsh conditions in winter than the larvae of species that are protected within the gall. Consequently, it could be argued that the populations of *N. anthracinus* are more subject to variations in the weather. This could explain the high level of synchrony in the population fluctuations of *N. anthracinus*, which were most probably caused by correlated weather along the transects (see below). Unfortunately no dispersal data are available for the species studied here. Nevertheless, it seems possible that at the small scale differences in dispersal behavior may be responsible for the different synchronies of the six species. At the large scale, however, dispersal may not be relevant. It seems unlikely that dispersal over several hundred kilometers would be sufficient to synchronize population dynamics, as occurred for *Neuroterus anthracinus*.

From studies on other insects it is known that synchrony may also be induced by environmental factors and biological interactions. In gall-maker species, synchrony or asynchrony may be caused by two possible factors: weather and parasitoids. However, the population dynamics of gall-makers on oak are generally not well understood (Stone *et al*. 2002). Additionally, high spatial variability in the underlying processes has been found (Hails & Crawley 1992).

At the small scale, it is probable that temperature and precipitation are quite homogeneous within the 8 km study transect, particularly because the study area is very flat and thus no relief-related differences are expected. So it seems unlikely that weather is responsible for the largely asynchronous fluctuations observed in some species. In the gall wasp *Neuroterus anthracinus*, a high degree of synchrony was found at both the small scale and the large scale. The fluctuations were similar over distances of several hundred kilometers. This high degree of synchrony was probably caused by synchronous meteorological factors throughout the entire transect across Germany. However, it is not impossible that these meteorological factors acted indirectly by influencing the parasitoid complex of this species.

Gall-makers are attacked by a number of specialist and generalist parasitoids (Stone *et al.* 2002). In all species except *Neuroterus anthracinus*, at the large scale the levels of synchrony were low and not distance-dependent. This asynchrony may be related to regional differences in parasitoid complexes. Such differences may result in spatially different population dynamics of the host. Interestingly, in Great Britain Schönrogge and Crawley (2000) found a decrease in the number of parasitoid species of oak gall wasps in the north of the country. At the small scale, the observed asynchrony in most species may also be related to the spatially heterogeneous effects of parasitoids. In a detailed study of population dynamics and mortality factors of the oak gall-maker *Andricus quercuscalicis*, Hails and Crawley (1991, 1992) found a high level of variability between individual trees and between years, which was mainly attributed to the attack rate of parasitoids.

REFERENCES

Biedermann R (2005) Incidence and population dynamics of the leaf beetle *Gonioctena olivacea* in dynamic habitats. *Ecography* **28**, 673–681.

Bjørnstad ON, Ims RA, Lambin X (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology and Evolution* **14**, 427–432.

Bonnet E, Van de Peer Y (2002) zt: a software tool for simple and partial Mantel tests. *Journal of Statistical Software* **7**, 1–12.

Bowman J, Forbes G, Dilworth T (2000) The spatial scale of variability in small-mammal populations. *Ecography* **23**, 328–334.

Buhr H (1965) *Bestimmungstabellen der Gallen (Zoo- und Phytocecidien) an Pflanzen Mittel- und Nordeuropas*, Vol. I–II. Gustav Fischer Verlag, Jena.

Buonaccorsi JP, Elkinton JS, Evans SR, Liebhold AM (2001) Measuring and testing for spatial synchrony. *Ecology* **82**, 1668–1679.

Cappuccino N, Price PW (1995) *Population Dynamics. New Approaches and Synthesis*. Academic Press, San Diego, CA.

Hails RS, Crawley MJ (1991) The population dynamics of an alien insect: *Andricus quercuscalicis* (Hymenoptera, Cynipidae). *Journal of Animal Ecology* **60**, 545–562.

Hails RS, Crawley MJ (1992) Spatial density dependence in populations of a cynipid gall-former *Andricus quercuscalicis*. *Journal of Animal Ecology* **61**, 567–583.

Hanski I, Woiwod IP (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology* **62**, 656–668.

Haydon D, Steen H (1997) The effects of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis. *Proceedings of the Royal Society of London Series B* **264**, 1375–1381.

Huffaker C, Berryman A, Turchin P (1999) Dynamics and regulation of insect populations. In: Huffaker CB, Gutierrez AP (eds) *Ecological Entomology*, pp 269–312. Wiley, New York.

Kampichler C, Teschner M (2002) The spatial distribution of leaf galls of *Mikkiola fagi* (Diptera: Cecidomyiidae) and *Neuroterus quercusbaccarum* (Hymnoptera: Cynipidae) in the canopy of a Central European mixed forest. *European Journal of Entomology* **99**, 79–84.

Kendall BE, Bjørnstad ON, Bascompte J, Keitt TH, Fagan WF (2000) Dispersal, environmental correlation, and spatial synchrony in population dynamics. *American Naturalist* **155**, 628–636.

Kindvall O (1996) Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology* **77**, 207–214.

Liebhold A, Kamata N (2000) Are population cycles and spatial synchrony a universal characteristic of forest insect populations? *Population Ecology* **42**, 205–209.

Lundberg P, Ranta E, Ripa J, Kaitala V (2000) Population variability in space and time. *Trends in Ecology and Evolution* **15**, 460–464.

McCullough DG (2000) A review of factors affecting the population dynamics of jack pine budworm (*Christoneura pinus pinus* Freeman). *Population Ecology* **42**, 243–256.

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (2000) Spatial synchrony in populations of birds: effects of habitat, population trend, and spatial scale. *Ecology* **81**, 2112–2125.

Pollard E (1991) Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos* **60**, 7–10.

Raimondo S, Liebhold AM, Strazanac JS, Butler L (2004) Population synchrony within and among Lepidoptera species in relation to weather, phylogeny, and larval phenology. *Ecological Entomology* **29**, 96–105.

Ranius T (2001) Constancy and asynchrony of *Osmoderma eremita* populations in tree hollows. *Oecologia* **126**, 208–215.

Ranta E, Kaitala V, Lindström J (1999) Spatially autocorrelated disturbances and patterns in population synchrony. *Proceedings of the Royal Society of London Series B* **266**, 1851–1856.

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Redfern M, Askew RR (1992) *Plant Galls*. Richmond Publishing, Slough.

Schönrogge K, Crawley MJ (2000) Quantitative webs as a means of assessing the impact of alien insects. *Journal of Animal Ecology* **69**, 841–868.

Steen H, Ims RA, Sonerud GA (1996) Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology* **77**, 2365–2372.

Stone GN, Schönrogge K, Atkinson RJ, Bellido D, Pujade-Villar J (2002) The population biology of oak gall wasps (Hymenoptera: Cynipidae). *Annual Review of Entomology* **47**, 633–638.

Sutcliffe OL, Thomas CD, Moss D (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology* **65**, 85–95.

Thomas CD (1991) Spatial and temporal variability in a butterfly population. *Oecologia* **87**, 577–580.

Williams DW, Liebhold AM (2000) Spatial synchrony of spruce budworm outbreaks in Eastern North America. *Ecology* **81**, 2753–2766.

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