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Time-traveling larvae ensure survival in small, synchronously fluctuating populations

CHRISTER SOLBRECK[1,†] AND OLOF WIDENFALK[1,2]

[1]*Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden*
[2]*Greensway, SE-756 51 Uppsala, Sweden*

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Abstract. Population structure is an important aspect of patchily distributed organisms. Small local populations, large temporal fluctuations, synchronized dynamics, and low migration rates should all lead to lowered rates of patch occupancy and increased extinction risks. These effects can, however, be counteracted if there is a pool of hidden, dormant individuals bridging unfavorable periods. Prolonged diapause—a dormancy that extends over two or more years—provides such a temporal bridge among insects, but its role in structuring patchy populations is poorly known. Based upon a long-term study, we explore the landscape scale population structure of a galling insect, the larva of which has an unusually long diapause spent hidden in the soil. Gall populations in patches fluctuated synchronously in a long wave with a tenfold amplitude. Abundances were very low with a median of less than twenty galls per patch. Although only a third of the patches had galls in all years, local populations persisted thanks to the pool of diapausing larvae. Colonizations of two new plant patches were very slow. The combination of small, synchronously fluctuating gall populations and high occupancy rates can be maintained because of the very low extinction rates imposed by the time-traveling diapausing larvae.

Key words: gall midge; occupancy; patchy populations; population density; prolonged diapause; swallow-wort.

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† **E-mail:** Christer.Solbreck@slu.se

INTRODUCTION

Population structure is an important aspect of patchy populations. For example, small local populations, large synchronous population fluctuations, and low inter-patch migration rates are all likely to lead to low rates of occupancy and population persistence. If, however, parts of the populations reside in some kind of seed bank or refuge hidden to the ecologist's eye, such effects can be nullified. Dormant individuals can then form an insurance against local extinctions, allowing local populations to persist despite low rates of colonization. Active cohorts may disappear for several years, by entering the hidden dormant stage. When they reemerge much later from the refuge, this is like being colonized in time (Chesson and Warner 1981, Hairston et al. 1996). Examples of such bridging mechanisms are provided by the soil seed banks of plants (Bulmer 1984, Klinkhamer et al. 1987, Thompson 2000), zooplankton resting stages in bottom sediments (Hairston 1996), and by prolonged diapause among insects (Hanski 1988).

Although most insects are short-lived, with one or several generations per year, some species have multi-year life spans. These extended life cycles can be the result of slow larval development or sometimes of long reproductive lives. In other cases, insects with short *active* lives are long-lived due to an extended dormancy period. This prolonged diapause usually involves just one or two extra years, but in extreme cases, the diapause may extend over more than a decade.

The prolonged diapause allows the insect to travel in time and track intermittent resource peaks or escape catastrophic years or enemies with shorter generation times (Danks 1987, 1992, Hanski 1988, Solbreck and Widenfalk 2012, Salman et al. 2016).

Effects of prolonged diapause on population structure in patchily distributed insects are very poorly known, especially so in species with an extra-long diapause. Prolonged diapause in insects differs from the analogous processes in plants and zooplankton with regard to some processes. For example, while germination or emergence in the latter mentioned groups often is the result of disturbance or other signals pertaining to environmental change (Thompson 2000), timing of insect emergence from diapause often seems to be predetermined at the time of entry into the dormant stage (Solbreck and Widenfalk 2012).

An important aspect of prolonged diapause is how it is coupled to the degree of synchrony of population change in different patches. If migration rates between local populations are low, fluctuations in these populations could potentially be uncoupled and asynchronous. Or synchrony would at least be expected to decrease rather steeply with inter-patch distance. However, it is also possible that local population is synchronized by interactions with more dispersive enemies or by correlated weather events (Moran 1953, Royama 1992, Liebhold et al. 2004).

The gall midge *Contarinia vincetoxici* is a patchily distributed insect with a very long diapause. It galls the flowers of the perennial herb *Vincetoxicum hirundinaria*. After a brief period inside the flower gall, the full-grown larvae fall to the ground where they enter a long diapause. We showed in a previous study that this diapause can last up to 13 yr with a median duration of at least six years (Solbreck and Widenfalk 2012). Field experiments further showed that recruitment from the pool of dormant larvae ensured local population survival even though all active stages were removed for several years (Solbreck and Widenfalk 2012). The host plant forms fairly discrete, long-lived, and widely spaced patches on the landscape scale. Because the insect is strictly monophagous, these patches also unambiguously define the habitat patches of the insect.

Here, we investigate the effects of the prolonged diapause of this insect in a large-scale patch system. Based upon censuses of galls in a landscape of 48 patches over a period of twelve years, we ask what are the patterns of occupancy, density fluctuations, and synchrony in gall density.

MATERIALS AND METHODS

Study area and organisms

White swallow-wort, *V. hirundinaria* Med. (Asclepiadaceae), is a long-lived, perennial herb. It grows in rocky areas as well as in more sheltered positions like forest margins. In Sweden, it occurs along the southeastern coast and on the islands of Öland and Gotland (Hultén 1971). The flowering period is extended. Usually, it begins in late May to early June and lasts until late July or August. Flower production is relatively constant from year to year (Ågren et al. 2008).

The study area at Tullgarn (58°57′ N, 17°36′ E) is situated on the Baltic coast about 50 km SSW of Stockholm, Sweden (Fig. 1). The presence of *V. hirundinaria* has been mapped in the 3 × 4 km study area since the late 1970s (Solbreck 2012).

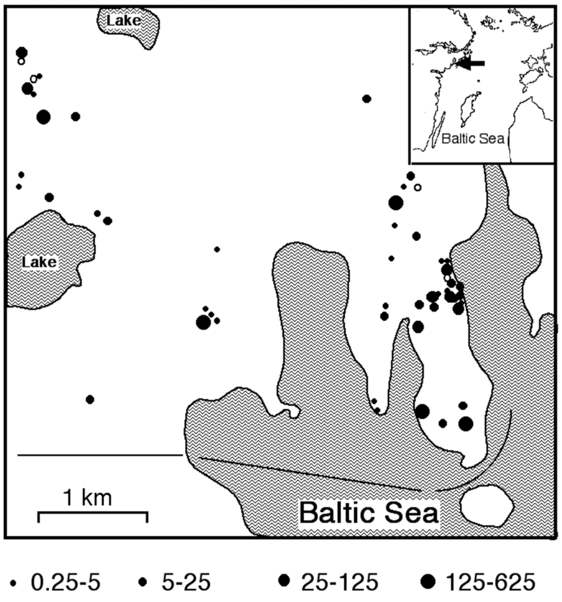

Fig. 1. Map of study area at Tullgarn showing locations and size classes (in m^2) of *V. hirundinaria* patches (1995–2006). Patches for which data on gall abundance are lacking are unfilled. Wave pattern shows lakes and the Baltic Sea. The line delimits the study area.

Plants are patchily distributed in the landscape forming 52 discrete patches (Fig. 1) with a mean size (for 1995–2006) of 26.7 m^2 (range 0.25–433). Patch size is measured as the ground area covered by the host plant. A patch is by our definition separated by at least 25 m from other *V. hirundinaria* individuals.

Adults of the gall midge *Contarinia vincetoxici* Kieffer (Diptera, Cecidomyiidae) are short-lived with a life span of at most a couple of days. Females oviposit in young flower buds of *V. hirundinaria,* which then develop into galls (Widenfalk et al. 2002). The gall is formed by the basally swollen and unopened petals. It is larger than an ordinary flower bud, and it usually has a reddish taint (Fig. 2). Each gall contains on average fifteen midge larvae, which feed in the gall for about two weeks. When fully grown, they leave the gall and spin a larval cocoon in the soil where they spend their long diapause (Solbreck and Widenfalk 2012). The adult females produce about thirty-five eggs, which means that they on average may induce two galls. Galls are usually found from the beginning of June until the end of July (Widenfalk et al. 2002).

Censuses of galls

All *V. hirundinaria* patches were visited once every week during the galling season. All new galls were counted on each visit and their location was indicated by an ink mark on the closest leaf in order to avoid double counts on later visits. Yearly totals of galls in each patch were calculated. Gall abundance measures are thus total censuses. There are two exceptions to this. For the two largest patches (171 and 433 m^2), only a part of the area was censused (13.9% and 15.4%, respectively) and the record corrected for total patch area (none of these patches had any zero values, cf below). Data from four small host plant patches (totaling 4.5 m^2 in area) were not used because of incomplete records (Fig. 1), leaving a total of 48 patches used in the analyses.

Since we will discuss local extinctions, the reliability of zero values needs comments. It is of course difficult to show that there is nothing of something as tiny as a gall midge. However, with regard to the galls, we think conditions are exceptionally good for obtaining reliable zeroes. Galls are easy to see, estimates are total censuses (with two exceptions), and most patches are

Fig. 2. *Vincetoxicum hirundinaria* flowers with two newly formed galls indicated by arrows.

small. Censuses are based on repeated visits, and galls remain for at least two visits.

To analyze the degree of synchrony in gall population change, log gall abundance for the time series 1995–2006 was calculated for 27 patches which had a total of at least 100 galls during the period and no more than two years with zero galls (zeroes were substituted by 0.5 galls). All pairwise correlations between the 27 time series were calculated and compared with inter-patch distances.

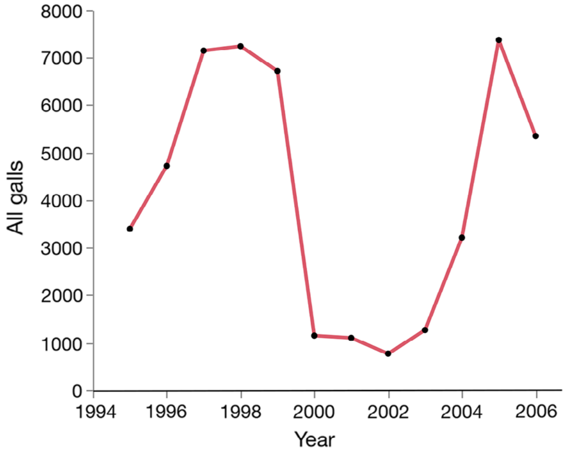

Fig. 3. Total gall abundance at Tullgarn 1995–2006.

Results

The total gall population of the 48 patches censused (Fig. 1) fluctuated in a wave-like fashion with a tenfold difference between maximum and minimum values during twelve years (Fig. 3). Fluctuations in gall abundance in the different patches are highly synchronous. Most pairwise correlation coefficients are strongly positive, and none is negative (Fig. 4). No significant decline in correlation with distance up to the maximum measured (5 km) was found (Fig. 4).

Gall abundance in plant patches is generally very low. Half of the patches have a mean abundance over the study period of less than 18 galls per year (range 0–803) and a peak value of 59 or less (range 0–1788). Almost all patches have had galls at least some years; of the 48 host plant patches studied, only four have been without galls all years (Table 1). These are all very small patches (0.25, 0.25, 0.55, and 2.5 m^2).

Two patches are undoubtedly recently colonized. They are small (both 0.25 m^2) and relatively newly established plant patches. One of the patches was colonized by 1 gall in 2005 and the other by five galls in 2006. This was 10 and 14 yr, respectively, after patch establishments. Both patches are close (50 and 170 m) to large inhabited patches.

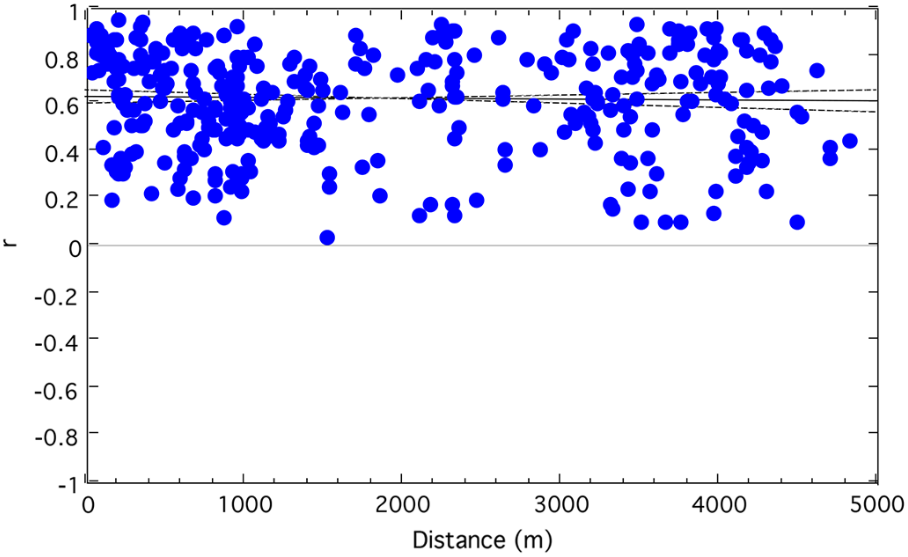

Fig. 4. Correlation coefficients for all pairwise correlations (N = 351) between log gall abundance time series (1995–2006) for 27 patches in relation to inter-patch distances. The regression line with 95% confidence intervals shows zero slope.

Table 1. Host plant patches at Tullgarn classified according to patterns of gall occurrence 1995–2006.

Pattern	No. host plant patches
Without galls all years	4
Colonization observed (new patches)	2
With galls all years	17
With galls some years	25

Only a third of the patches (17) have had galls all years, whereas a majority (25) have had galls some years but not all (Table 1, Fig. 5). A common picture for these populations is that their population peaks coincide with peaks in the patches without zeroes and that their zeroes coincide with the general population valley.

Discussion

Prior field experiments had given direct evidence of the extended diapause in *C. vincetoxici* larvae (Solbreck and Widenfalk 2012). The emergence from an experimental cohort was spread like a long wave over more than ten years. Furthermore, long-term gall removal had no detectable effect on either gall density or fluctuation pattern for over a decade, indicating that recruitment from the long-lived refuge totally dominated gall dynamics.

The present study shows that fluctuations in gall abundance are of the same large, long-wave character also on the landscape scale. It also shows that almost all patches seem to be continually inhabited, despite the small gall populations and low rates of colonization (see below). Fluctuations in gall abundance are highly synchronous in the different patches and with numerous zero counts. Zeroes occur in years with generally low densities and undoubtedly represent pseudoextinctions rather than true extinctions.

The hidden and sleeping part of the population is evidently considerably larger than the observed gall population, and the generally low abundance of galls in host plant patches gives a false image of true population size. Although most patches have one or more years without galls, they are evidently continually inhabited. Patches with zero galls have the same fluctuation pattern as those which do not have zeroes, with no evidence of lags in population buildup following zero gall years (Fig. 5).

Theoretically, the same pattern of gall occurrence could be maintained by a high colonization rate, but this is highly unlikely in *C. vincetoxici*. Adult midges are tiny, fragile, and very short-lived insects with poor colonization ability. Although gall midges may enter the aeroplankton and travel by winds (Johnson 1969), their power of upwind flight is very limited (Sylvén 1970). In this study, two new host plant patches were naturally established. It took 10 and 14 years, respectively, before they were colonized, despite the fact that they were close to other large inhabited patches. In colonization experiments in other areas (Widenfalk and Solbreck, *unpublished data*), we have yet not observed any colonizations. We conclude that colonization rates are very low, that true extinctions are rare, and that the vast majority of patches have been continually inhabited for many years.

Such a demographic structure may impact the genetic composition of populations (Suez et al. 2013). Whereas low colonization rates and low local densities are expected to cause loss of genetic variation, prolonged diapause is expected to preserve genetic variation. Population genetics studies of *C. vincetoxici* reveal a genetic structure indicative of low gene flow between populations (Laugen, Cassel-Lundhagen and Solbreck, *unpublished data*).

There is strong synchrony between patches in the temporal pattern of gall density change (Figs. 4, 5). This is surprising for patches not linked by much migration. Furthermore, a species with extended diapause should be buffered against years with extreme weather and hence be unlikely to be directly synchronized by weather events as suggested by the Moran effect (Moran 1953). Indeed, prolonged diapause is often thought to have evolved in response to such unpredictable disturbances. However, it is possible that interactions with more dispersive enemy populations may synchronize gall populations. Two oligophagous parasitoid species attack *C. vincetoxici* larvae at fairly high rates (Widenfalk et al. 2002, Solbreck and Widenfalk 2012). Coupled host–parasitoid systems involving prolonged diapause have been shown to produce long population waves (Ringel et al. 1998). We

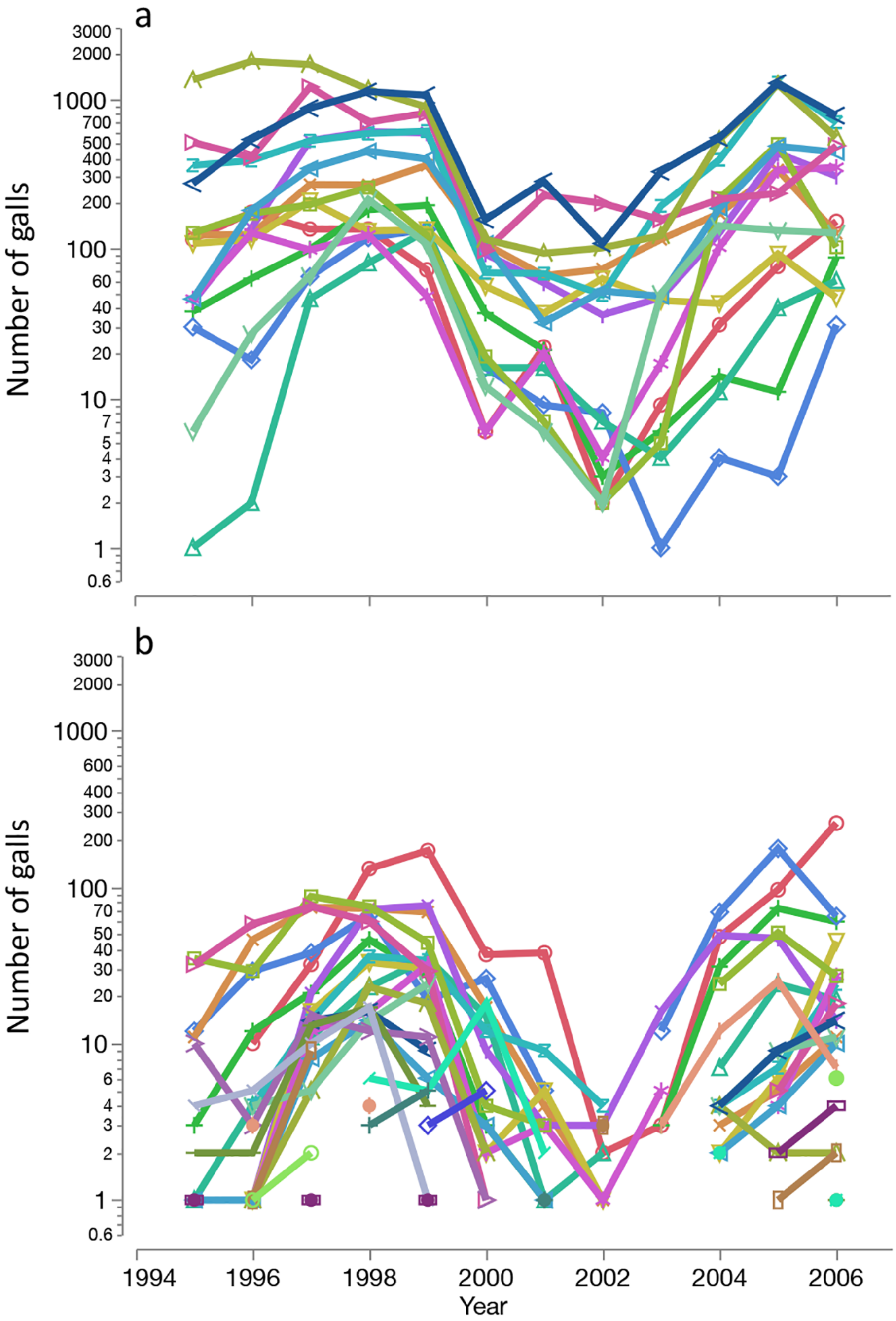

Fig. 5. Fluctuation patterns of galls in (a) patches which had galls in all years and (b) patches which lacked galls one or more years.

hypothesize that dispersive oligophagous parasitoids are synchronizing the waves observed in *C. vincetoxici* populations. Resource changes are highly unlikely to affect gall fluctuations, because the abundance of flowers is fairly constant from year to year (Ågren et al. 2008), and even in peak gall years less than 0.5% of flowers are galled (Widenfalk et al. 2012).

Our study illustrates how high occupancy rates can be maintained in a patchy population despite (seemingly) small local population sizes and large synchronous temporal fluctuations. Prolonged diapause allows the insect to travel in time bridging the gaps of pseudoextinctions. Another way to view the situation is that ecologists easily miss the true picture of population size if they are ignorant to long-lived hidden population cohorts.

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