

Colonisations and extinctions at multiple spatial scales: a case study in monophagous herbivores

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Many plant–insect interactions show spatial structure at a hierarchy of scales. We investigate population turnover at different spatial scales in two specialist insect herbivores that feed on tansy, *Tanacetum vulgare*, in the Tvärminne archipelago in south-western Finland. Colonies of both aphid species form on individual ramets and in addition to the level of ramets, individuals cluster at the levels of the genet, groups of plants, and islands in the archipelago. Colonisations and extinctions were observed at all spatial levels studied. Mean persistence times in both species ranged from less than five weeks at the level of the ramet to less than 20 weeks at the level of islands, such that aphids over-wintered on only a fraction of the islands in the archipelago. Our field study suggests that aphids on tansy form a hierarchically structured metapopulation where longer-term persistence is only possible at the level of the archipelago.

Introduction

A metapopulation structure has been described for many herbivorous insects, in particular in butterflies (e.g. Hanski 1999, Doak 2000a, 2000b, Menéndez & Thomas 2000, Roland *et al.* 2000), but also in beetles (Whitlock 1992, Verdyck & Desender 1999, Roslin 2000) and a variety of other insect orders (Eber & Brandl 1996, Hanski 1999, Weisser 2000). Because insect herbivores are dependent on their host plant, their spatial distribution is closely linked to the distribution of their host plant. As plants form discrete units in space, often occurring in groups and generally having a patchy regional distribution, individuals of a particular species of insect herbivore naturally

aggregate at different spatial scales (e.g. Dempster *et al.* 1995a, 1995b, Johannesen & Loeschcke 1996, Verdyck & Desender 1999, Doak 2000a, 2000b). For example, many insect herbivores feed on particular structures of a plant, such as leaves or shoots. A single plant (genet) consists of several such modules and, consequently, there is already spatial structuring at the level of a single plant. Depending on the spatial distribution of the plant, there may be a number of higher levels at which plants and hence the herbivores cluster. If plants occur singly and are widely spaced like trees in a savannah, the next higher spatial level may be the regional scale. In contrast, if plants occur in groups, then the group of plants is the next spatial level at which individuals cluster. In

such hierarchically aggregated plant–herbivore systems, extinctions can occur at all spatial scales (e.g. Solbreck & Sillen-Tullberg 1990, Dempster *et al.* 1995a, Menendéz & Thomas 2000). Yet, most metapopulation studies have, so far, concentrated on larger spatial scales and less on the level of single plants or groups of plants (e.g. Doak 2000b, Menendéz & Thomas 2000).

Aggregations of individuals at the level of individual plants or groups of plants are most often examples of within-population spatial patchiness, not of metapopulation dynamics. In these cases, only one generation develops in an individual resource patch or the emerging adults from the different resource patches mix freely within a larger area such that they belong to the same local breeding population (Harrison 1991, Harrison & Taylor 1997, Hanski 1999). Such small-scale spatial aggregations can have important consequences for the dynamics of local populations, independent of any metapopulation dynamics (Atkinson & Shorrocks 1981, Hassell 2000). For example, small-scale aggregation of individuals in competing species may lead to the coexistence among two species that would not be able to coexist without such aggregation (Atkinson & Shorrocks 1981). Similarly, spatial variation in the risk of being attacked by a parasitoid can stabilize host–parasitoid interactions (Hassell 2000). A critical difference between such within-population spatial patchiness and metapopulation dynamics is that in the former case the population does not go extinct and is not necessarily coupled with other populations through migration.

When the host plant is a long-living perennial herb or a tree, it is possible that multiple generations of individuals occur at the level of a single plant (cf. Gripenberg & Roslin 2005). In this case, a metapopulation approach to understand the population ecology of the herbivore species might or might not be useful, and detailed studies are necessary to determine whether local breeding populations indeed persist over several generations and whether there are extinctions and colonisations at the level of independent populations. Because in hierarchically clustered organisms the existence of spatial variation within populations does not preclude true metapopulations dynamics at a higher spatial level (and *vice versa*), it is necessary to study the different spatial levels

simultaneously, in order to investigate whether ecological processes take place both at a local and a metapopulation scale (Hanski 1999).

One example where multiple generations of individuals live on the same plant are aphids (Homoptera: Aphididae) (Addicott 1978, Dixon 1998). In the temperate region, aphids survive cold winters as eggs and first-generation females hatch from the hibernating eggs in spring to produce viviparous parthenogenetic daughters, which themselves reproduce asexually. The asexual cycle continues until the autumn when a short photoperiod and low temperatures induce the production of sexual females and males, which then mate to produce diapausing eggs (Dixon 1998). During the asexual phase, females are either winged or wingless, and in many species the winged dispersal morphs are primarily induced by adverse environmental conditions (Dixon 1998, Weisser *et al.* 1999, Müller *et al.* 2001). Because of parthenogenetic reproduction and a short developmental time, aphid colonies form rapidly on the shoots, roots or leaves of plants (Dixon 1985). In addition, growing colonies consist mostly of wingless individuals that show limited movement, which further enhances the aggregation of individuals at the level of an aphid colony. While aphid infection reduces plant fitness through the extraction of nutrients and the transmission of plant viruses even to the extent that the plant dies (Minks & Harrewijn 1987), many perennial herbs and trees sustain long periods of aphid infestation in the field (Addicott 1978, Dixon 1998). Thus, it appears that in plant–aphid systems independent local populations may occur at the level of individual colonies (cf. Addicott 1978). However, most studies of aphid population ecology have so far been performed at higher spatial levels with little reference to metapopulation dynamics. Moreover, they have largely focused on agricultural host–aphid systems (Addicott 1978, Dixon 1985, 1998, Minks & Harrewijn 1987, Massonnet *et al.* 2002).

In this paper, we investigate the population ecology of two specialist aphid species, *Metopeurum fuscoviride* Stroyan and *Macrosiphoniella tanacetaria* Kaltenbach (Homoptera: Aphididae), both monophagous on the common tansy (*Tanacetum vulgare* L., Asteraceae). Tansy is a tussock-forming, perennial hemicryptophyte

native to Europe and Asia that originally occurred along rivers (Mitch 1992). A single tansy plant (= genet) consists of several shoots (= ramets). In both aphid species, colonies form at the top of individual shoots. *M. fuscoviride* colonies are ant-tended whereas colonies of *M. tanacetaria* are not (Fischer *et al.* 2001). Both aphid species produce both winged and wingless morphs during the asexual phase. While the egg-laying sexual females in both species are unwinged, the males of *M. tanacetaria* are winged and the males of *M. fuscoviride* are unwinged. Previous studies have shown that in central Europe, where tansy nowadays mostly occurs in disturbed areas such as wastelands or along roads and railway tracks, extinction rates at the level of individual colonies are very high (Weisser 2000, Massonnet *et al.* 2002). In mainland Scandinavia, tansy grows both in its natural habitat as well as in disturbed habitats. One area where the plant still occurs naturally is the archipelago of the Baltic Sea. To study the population ecology of the two species at the different spatial levels of (i) ramets, (ii) genets, (iii) groups of plants, and (iv) entire islands, we selected a number of islands in the Tvärminne archipelago in south-western Finland. Here, we ask whether there is population turnover at different spatial scales. Our main approach was to individually mark all plants on a number of islands (1) to study colonisations, extinctions and changes in the number of individuals at the four spatial scales over the time-course of a season, (2) to analyse dispersal patterns by studying the occurrence of winged morphs in aphid colonies, and (3) to analyse if extinctions are caused by host plant deterioration or interaction with natural enemies.

Material and methods

Study area

The study area was the Tvärminne archipelago in the southern Gulf of Finland, in the immediate vicinity of Tvärminne Zoological Station of the University of Helsinki, Finland (59°50'N, 23°14'E). Most of the islands belong to the Tvärminne Zoological Station or to the Jusarö Strict Nature Reserve (Halkka *et al.* 1971).

These islands are protected and human impact is relatively low. In particular, tansy genets are not mown on any of the islands, as it is the case in many disturbed areas throughout Europe where tansy occurs. The archipelago is a dynamic system. Land upheaval, caused by the melting of the continental ice shield 8000 years ago, amounts to about 42 cm in 100 years (Halkka *et al.* 1971). New islands are constantly emerging and the existing ones grow in size. The vegetation of the islands depends on island age and size. In the Tvärminne archipelago, the eggs of both *M. fuscoviride* and *M. tanacetaria* hatch between the end of May and the end of June, and sexual morphs can be observed from the beginning of August (W. W. Weisser unpubl. data).

In June 2001, eight islands were chosen according to the following criteria: (i) presence of *M. fuscoviride* and/or *M. tanacetaria* directly after egg hatch, (ii) fewer than 300 tansy genets, and (iii) accessibility by motorboat within a few minutes from Tvärminne Zoological Station. The eight selected islands were Algrundet 3 (AL3), Furuskär (F), Fyrgrundet (FY), Halsholmen (HH), Porsgrundet (P), Rovholmarna (R), Storgrundet (ST), and a small island labelled AB, all in the vicinity of Tvärminne Zoological Station (Fig. 1). These eight islands are later referred to as initially colonised islands.

In order to study the colonisation of empty islands, ten islands were chosen where no aphids were found until the end of June (a time when colonies on the initially colonised islands were already quite large in size). Additional selection criteria were the vicinity to Tvärminne Zoological station and a moderate number of tansy genets (< 30). These islands, Mellanskär (M), SMF, N1, Vindskären 3 (VI3), Alören (AÖ), Fyrgrundet 2 (FY2), AL4, HH1, J2 and Kvarnskär (KV) (Fig. 1), are referred to as initially uncolonised islands.

Before the start of the study, the location of all plants on the islands was noted on maps of the islands. Plants were allocated into groups based on the criterion that two genets growing less than 5 m apart belong to the same group. The 5-m criterion was based on observations that indicate that aphids are unlikely to colonise another genet by walking if the distance is greater than 5 m (W. W. Weisser unpubl. data).



Fig. 1. A map of the study area with all islands included in the survey. The eight initially colonised and the ten initially uncolonised islands are labelled (AL3 = Algrundet, AÖ = Alören, F = Furuskär, FY = Fyrgrundet, FY2 = Fyrgrundet 2, HH = Halsholmen, KV = Kvarnskär, M = Mellanskär, P = Porsgrundet, R = Rovholmarna, ST = Storgrundet, VI3 = Vindskären 3), for all other labelled islands there was no full name. Islands where tansy did not occur are marked white, and islands where the host plant occurred but where no aphids were observed are shaded in grey. On islands marked in black both tansy and aphids were present. Islands not labelled with their name formed part of a larger study where the presence of aphids on islands in the Archipelago was investigated (S. A. Härrä *et al.* unpubl. data).

Population dynamics of tansy aphids

Starting on 20–22 June 2001 (= week 1) all ramets of all tansy genets on the initially colonised islands were inspected weekly for the presence of aphids. Each ramet where aphids were found was labelled individually. In addition to the presence of aphid species, the phenological state of the ramet (shoot, bud, flower, withered, seed, crippled, dead), the size of the aphid colony, the occurrence of natural aphid enemies (ladybirds, spiders, etc.), and of winged individuals or fourth instar larvae with wing buds was recorded. Aphid colony size was estimated as follows: for *M. tanacetaria*, all individuals feeding on a ramet were counted when the plant was

visited to obtain a field count. For *M. fuscoviride*, a field count was obtained for small colonies whereas for larger (> 100 individuals) colonies, the length of the colony was measured with a ruler. The length of the colony was converted into colony size using the equation:

$$\text{No. of aphids in colony} = 112.8 \times \text{Length of colony (cm)} - 7.9$$

based on the sampling of 50 colonies that were first measured in the field and later counted under a microscope ($r = 0.93$, $p < 0.001$). Similarly, for both aphid species the field counts were converted into colony size estimates using the equations:

$$\begin{aligned} M. fuscoviride: y &= 2.37x - 0.25, \\ (r &= 0.81, p < 0.001, N = 50). \end{aligned}$$

$$\begin{aligned} M. tanacetaria: y &= 1.96x - 0.25, \\ (r &= 0.93, p < 0.001, N = 50). \end{aligned}$$

where x is the counted colony size and y is the corrected colony size (based on the sampling of 50 colonies that were first counted in the field and later counted under a microscope).

Genets were inspected until week 20 (2–5 November 2001) when no more *M. tanacetaria* or *M. fuscoviride* were observed, i.e. when all colonies were extinct. Until week 13, the survey was done weekly; thereafter, ramets were checked only every second or third week.

The ten initially uncolonised islands were visited every two weeks and each ramet was inspected for the presence of aphids. In contrast to the initially colonised islands, only the genet was labelled and the number of aphid colonies per genet and the total number of individuals per genet were counted, using the same methods as described above.

Statistical analyses

All statistical analyses were performed with SPSS 11.0. Means were compared using either t -tests or Mann-Whitney U -test if data did not meet assumptions for parametric tests. Associations between variables were examined with correlation analyses: for parametric tests, we report Pear-

son's moment product correlation coefficients, for non-parametric analyses we report Spearman's rank correlation coefficients. Throughout the manuscript, average values are presented as means with associated standard errors (SEM).

Results

Tansy on islands

On average, 3.5 ± 0.6 groups (range 1–9 groups), 43.4 ± 16.9 genets (5–292) and 505.2 ± 160.7 ramets (12–2686) occurred on each of the 18 studied islands (Table 1). The phenology of tansy was nearly identical on all islands. The first flowers appeared from weeks 4–6 and flowers were seen until week 18 (Fig. 2). Ramets started to set seeds 3 to 5 weeks later, although in general, only a small number of ramets produced seeds (Fig. 2). After seed set, tansy ramets started to die. A low number of new ramets appeared throughout the season and ramets that were still green were observed until the time when the last aphid died in November (Fig. 2). Some plants died during the season due to drought but the percentage of plants dying before seed set was low (Fig. 2).

Occupancy and number of aphids at different spatial scales

The data on aphid colonisations, persistence and extinctions at the spatial level of ramets, genets and groups for the 18 islands included in the seasonal survey are summarised in Table 1. A maximum of 12 islands was occupied simultaneously, 11 islands were colonised by *M. fuscoviride* and seven by *M. tanacetaria* (Table 1). On all islands where *M. tanacetaria* was present, *M. fuscoviride* was also present at least once during the season, except for VI3. Occupancy of islands and groups of plants changed frequently over the time course of the season (Fig. 3a and b). Occupancy on genets and ramets was low, with less than 15% of genets and 5% of ramets occupied at any one time (Table 1, Fig. 3c and d). For *M. fuscoviride*, occupancy first increased and then decreased, whereas for *M. tanacetaria*, there was a slight depression in occupancy during mid summer.

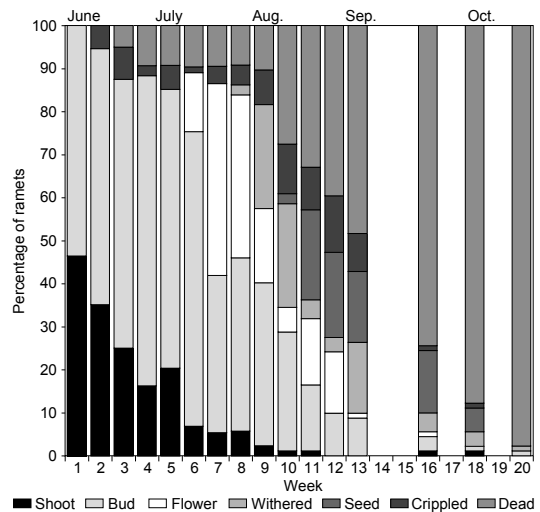


Fig. 2. Phenology of tansy on islands, here shown for the island AL3 ($N = 146$ genets).

The number of aphids counted at the level of islands showed the same overall trend on all initially occupied islands, with a maximum in August–September and a fast decrease at the end of the season (Fig. 4). In *M. tanacetaria*, there was a depression in population size on all islands in July, whereas no such pattern was observed in *M. fuscoviride* (Fig. 4). Overall, however, the total number of individuals was remarkably stable, varying only tenfold on many islands for a remarkably long period (Fig. 4). On average, 29250 ± 5596 individuals of *M. fuscoviride* were present on all the initially colonised islands per week, which was significantly higher than the weekly average of 5180 ± 1304 for *M. tanacetaria* ($U = 41$, $N = 30$, $P = 0.003$). On ramets, colony sizes ranged from 1 to 1400 individuals in *M. fuscoviride* and from 1 to 491 individuals in *M. tanacetaria*. Colonies of the ant-tended *M. fuscoviride* were on average larger than colonies of *M. tanacetaria* (Fig. 5), but again there was remarkable temporal constancy in mean colony size, measured across all occupied ramets.

Occurrence of dispersers and sexual morphs

Winged asexual individuals of *M. fuscoviride* occurred only from weeks 1 to 9 and few winged

Table 1. Plant occurrence and aphid colonisation, extinction and population size on the islands included in the field study. Initially colonised islands: Halsholmen (HH), Furuskär (F), Fyrgrundet (FY), Storgundet (ST), Rövholmarna (R), AL3, AB and Porsgrundet (P). Initially uncolonised islands Mellanskär (M), V13, N1, SMF, Ålbren (ÅÖ), HH1, AL4, Kalvholmen (KV), J2 and Fyrgrundet 2 (FY2). Col. week: week of colonisation, Ext. week: week of extinction. Persistence was measured at the level of ramets, genets and groups. On the initially uncolonised islands no data were collected at the level of ramets. Enemies include all predators and parasitoids of aphids that were observed on the ramets.

Island	No. of plant groups	No. of genets	No. of ramets	Metopeurum fuscoviride							Macrosiphoniella tanacetaria							No. of ramets with enemies		
				Col. week	Ext. week	Max. no. of groups colonised	Max. no. of genets colonised	Max. no. of ramets colonised	Mean survival groups (weeks)	Mean survival genets (weeks)	Mean survival ramets (weeks)	Col. week	Ext. week	Max. no. of groups colonised	Max. no. of genets colonised	Max. no. of ramets colonised	Mean survival groups (weeks)		Mean survival genets (weeks)	Mean survival ramets (weeks)
HH	6	292	2686	1	16	3	58	189	7.7	5.1	4.11	1	18	3	29	36	7.3	2.3	1.9	88
F	8	30	416	6	13	1	2	2	7	6	6	1	20	3	14	81	8.8	6.3	2.5	121
FY	6	42	348	9	16	1	3	3	6	4	4	1	20	1	18	104	18.5	9.3	4.1	192
ST	3	32	684	5	16	1	2	2	10	3	2.8	1	18	2	16	117	8.8	4.4	2.1	39
R	9	93	1072	5	16	4	5	5	4	2.6	2.8	1	20	3	23	115	11.6	6.0	3.0	61
AL3	3	146	1579	1	20	2	12	74	12.8	7	5.5	—	—	—	—	—	—	—	—	36
AB	1	26	151	1	16	1	20	82	14	6.9	5.5	—	—	—	—	—	—	—	—	77
P*	2	17	90	1/6	3/9	1	1/1	2/1	2.5	2.5	2	—	—	—	—	—	—	—	—	—
M	1	12	152	4	12	1	2	3	7.5	6.5	no data	4	8	1	6	6	3.5	1.8	no data	—
V13	6	22	137	—	—	—	—	—	—	—	—	4	18	3	9	25	11.2	5.7	no data	6
N1	5	13	564	4	10	1	2	2	5.5	3.5	no data	—	—	—	—	—	—	—	—	—
SMF	2	5	103	8	12	1	1	1	3.5	3.5	no data	—	—	—	—	—	—	—	—	—
AO	2	5	48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HH1	1	16	622	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AL4	2	7	141	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
KV	2	5	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
J2	2	7	29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
FY2	2	11	259	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* The island Porsgrundet was colonised twice.

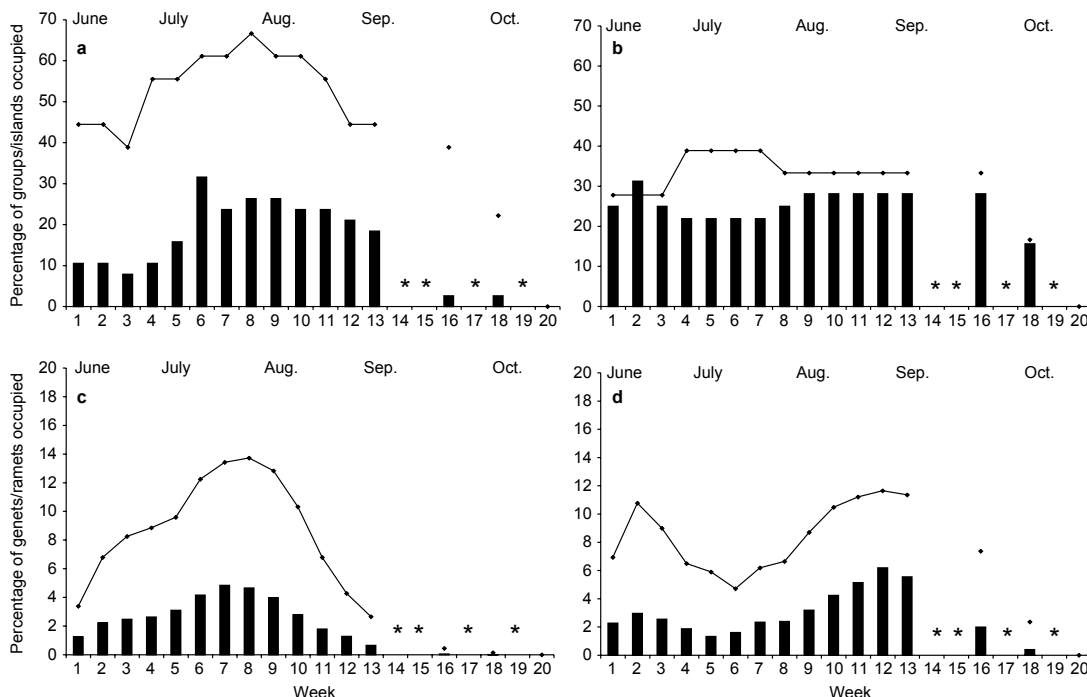


Fig. 3. Occupancy at the different spatial levels. The percentage of islands (lines) and groups (bars) occupied per week by (a) *M. fuscoviride* and (b) *M. tanacetaria*. The total number of groups was 38 for *M. fuscoviride* and 32 for *M. tanacetaria*. For the islands, the data from the initially uncolonised islands were also included ($N_{\text{islands}} = 18$). The asterisks mark weeks where no data were collected. The percentage of ramets (bars) and genets (line) on initially colonised islands that were occupied by (c) *M. fuscoviride* and (d) *M. tanacetaria*. $N = 678$ genets and $N = 7026$ ramets.

individuals were observed on the initially uncolonised islands which were colonised later in the season. Overall, winged individuals accounted for only 0.4% of all individuals from all weeks, with a mean proportion of $5.6\% \pm 0.5\%$ in colonies with winged individuals. However, in the weeks where winged individuals were found, winged individuals and/or fourth instar larvae with wing buds were present on average on 53% of occupied genets and on 44% of all occupied ramets.

For *M. tanacetaria*, the picture was similar with only 209 winged *M. tanacetaria* (0.3% of all individuals) observed throughout the survey (mean proportion $11.5\% \pm 1.4\%$ of individuals in colonies with winged morphs). Winged *M. tanacetaria* individuals were found from weeks 1 to 16, but after week 9, all winged individuals were males. On average, winged morphs and/or fourth instar larvae with wing buds were present on 17% of ramets and 29% of genets in the weeks

when winged individuals occurred. In *M. fuscoviride* the proportion of winged morphs was weakly negatively correlated with aphid colony size (only colonies with winged morphs: $r_s = -0.60$, $N = 337$, $P < 0.001$, all colonies: $r_s = 0.06$, $N = 2521$, $P = 0.004$). In *M. tanacetaria*, the proportion of winged morphs was also weakly negatively correlated with colony size (colonies with winged individuals: $r_s = -0.94$, $N = 140$, $P < 0.001$, all colonies: $r_s = 0.13$, $N = 3093$, $P < 0.001$).

The first males of *M. fuscoviride* and *M. tanacetaria* were observed in the beginning (week 7) and middle of August (week 9) respectively. The first sexual *M. fuscoviride* and *M. tanacetaria* females were observed in weeks 8 and 9, respectively. From mid-September (week 13) onwards, all females in both species were sexual, as shown by dissections of individuals collected in the field.

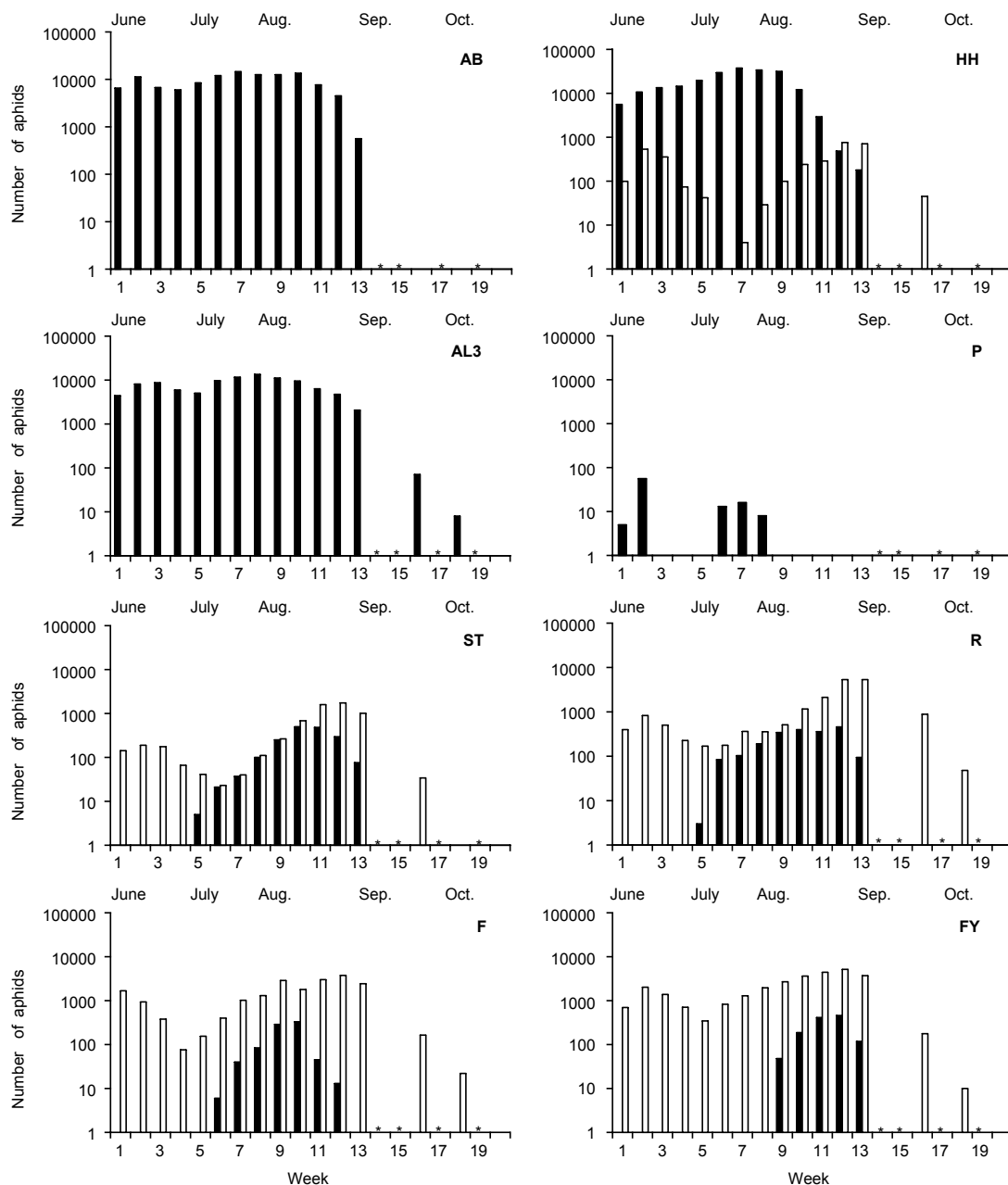


Fig. 4. The number of *M. fuscoviride* (black bars) and *M. tanacetaria* (open bars) on all eight initially colonised islands (Table 1). The weeks where no data were collected are marked with an asterisk. (HH = Halsholmen, P = Porsgrundet, ST = Storgrundet, R = Rovholmarna, F = Furuskär, FY = Fyrgrundet).

Persistence, colonisations and extinctions at different spatial scales

The constancy in mean occupancy and the total number of aphids at the various spatial levels

was not matched by the persistence times in the plant–herbivore system. Due to the duration of the field study, maximum persistence at any spatial level was 19 weeks. Realised survival was, however, much lower, with mean persist-

ence times of less than five weeks at the level of ramets, less than six weeks at the level of genet and between 8–11 weeks at the level of groups (Fig. 6a). Both at the level of ramets (Fig. 6b) and genets (not shown), the most common persistence time was one week. At the level of ramets, *M. fuscoviride* persisted for a shorter time than *M. tanacetaria* ($U = 239\,492$, $N = 1857$, $P < 0.001$), whereas both at the levels of genets ($t = 0.1$, d.f. = 415, $P = 0.926$) and groups ($U = 120$, $N = 32$, $P = 0.761$), there was no significant difference in survival time between the species. At the level of islands, *M. tanacetaria* survived slightly longer than *M. fuscoviride* ($t = 2.6$, d.f. = 12, $P = 0.023$, Fig. 6a).

Colonisations occurred at all spatial levels throughout the season (Fig. 7 and Table 1). Most newly colonised islands were colonised relatively early in the season. In *M. fuscoviride*, the last colonisation of an initially uncolonised island took place in week 9 in August whereas in *M. tanacetaria* all colonisations took place in the first week of the survey (Table 1 and Fig. 7 bottom row). At the level of groups, colonisations occurred in both species up to week 9. Thus, colonisations of groups and islands occurred in both species only within the period where winged females were observed in aphid colonies. At the level of ramets and genets, an initial decrease in the frequency of colonisations was observed for both aphid species, followed by an increase to a peak in July (*M. fuscoviride*) or August (*M. tanacetaria*), and a second decrease

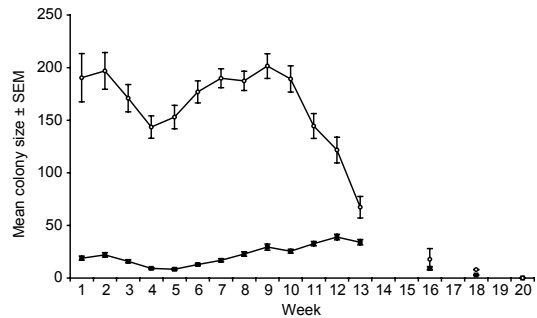


Fig. 5. Mean colony size (with SEM) on ramets of *M. fuscoviride* (open circles) and *M. tanacetaria* (black triangles) on the initially colonised islands. $N = 678$ genets and $N = 7026$ ramets.

for both species until the end of the season (Fig. 7 top row).

Extinctions also took place throughout the season, at all spatial levels (Fig. 8 and Table 1). At the island level, extinctions of *M. fuscoviride* occurred throughout the season, whereas all extinctions in *M. tanacetaria* were observed towards the end of the season (Fig. 8 bottom row). At the level of groups, there were extinctions both early and late in the season, in both aphid species. At the level of ramets and genets, most extinctions in both species occurred before plants set seeds and died. In *M. tanacetaria*, about 35 percent of all extinctions happened in late September and October. In *M. fuscoviride* this proportion was about 10%, as most extinctions were observed in August–early September (Fig. 8 top row). Taken together, the data on

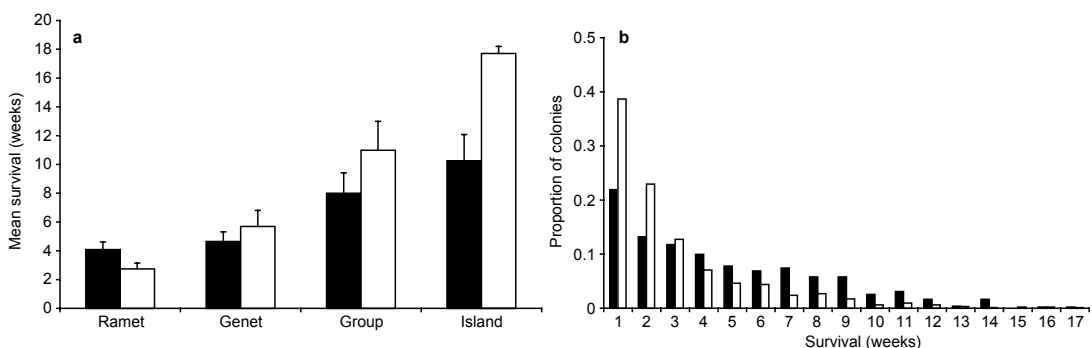


Fig. 6. Persistence at different spatial levels of *M. fuscoviride* (black bars) and *M. tanacetaria* (open bars). — **a:** Persistence at ramet, genet, group and island level. For each island, mean survival time was calculated and these means were averaged over the islands occupied by either species (*M. fuscoviride*: $N_{\text{islands}} = 8$, *M. tanacetaria* $N_{\text{islands}} = 5$). — **b:** Frequency diagram of survival times at the level of ramets. (*M. fuscoviride* $N = 553$, *M. tanacetaria* $N = 1304$).

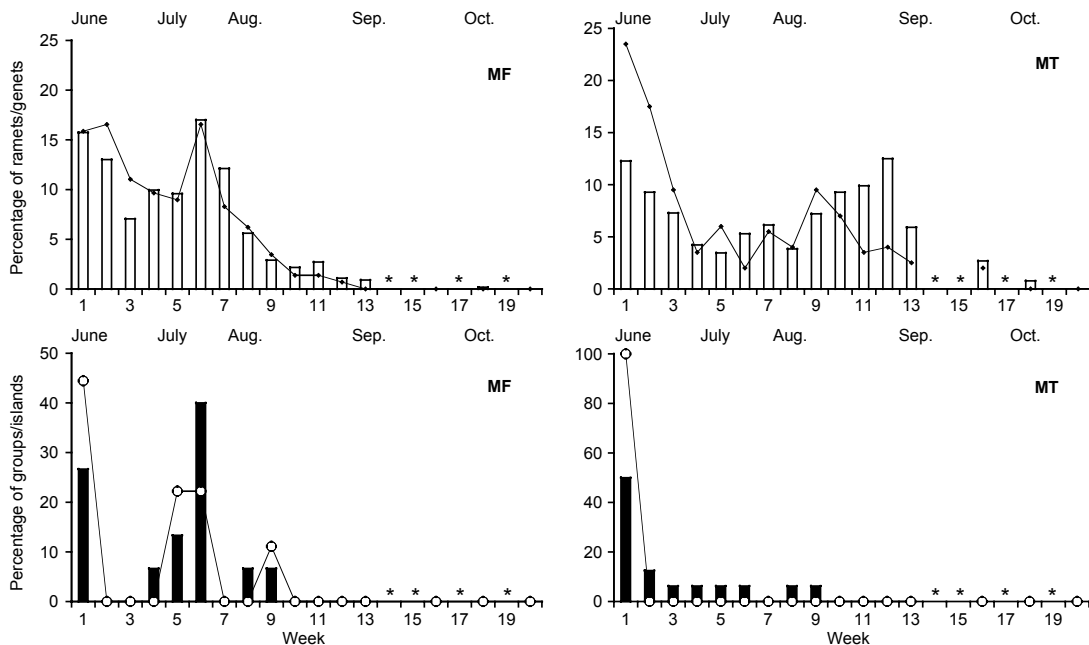


Fig. 7. Colonisations of *M. fuscoviride* (MF) and *M. tanacetaria* (MT) at the spatial scale of ramets ($N_{MF} = 553$, $N_{MT} = 1304$; open bars), genets ($N_{MF} = 145$, $N_{MT} = 200$; black squares), groups ($N_{MF} = 15$, $N_{MT} = 16$; black bars) and islands ($N_{MF} = 9$, $N_{MT} = 5$; open circles).

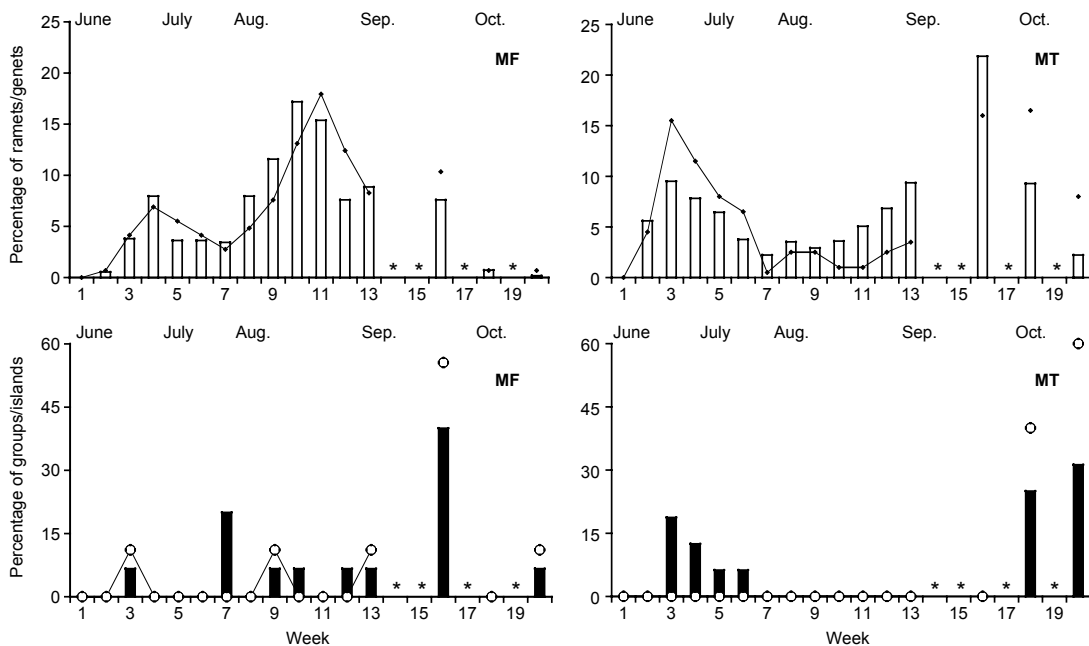


Fig. 8. Extinctions of *M. fuscoviride* (MF) and *M. tanacetaria* (MT) at the spatial scale of ramets ($N_{MF} = 553$, $N_{MT} = 1304$; open bars), genets ($N_{MF} = 145$, $N_{MT} = 200$; black squares), groups ($N_{MF} = 15$, $N_{MT} = 16$; black bars) and islands ($N_{MF} = 9$, $N_{MT} = 5$; open circles).

aphid persistence, colonisations and extinctions show that turnover rates at all spatial scales were very high.

For *M. fuscoviride*, persistence at the level of ramets was positively correlated with the size of the propagule colonising the ramet (size of colony in first week), although the correlation was relatively weak ($r = 0.28$, $P < 0.001$, $N = 553$). Survival was positively correlated with the maximum size of the colony ($r = 0.72$, $P < 0.001$) and with its mean size ($r = 0.63$, $P < 0.001$, $N = 553$). For *M. tanacetaria*, propagule size ($r = 0.1$, $P < 0.001$), maximum colony size ($r = 0.58$, $P < 0.001$), and colony mean size ($r = 0.4$, $P < 0.001$, $N = 1304$) all positively correlated with persistence at the level of ramets. The three colony size measures (size of colony at colonisation, mean and maximum colony size) were all positively correlated among each other ($P < 0.001$ in each case).

Natural enemies and causes for colony extinction

The number of natural enemies observed in aphid colonies was very low (Tables 1 and 2).

The three main groups of enemies were

ectoparasitic mites (*Thrombiidae*) which were observed mostly at the beginning of the season, insect predators (hoverfly larvae, ladybird adults and larvae, lacewing and aphid midge larvae) and parasitoids (Hymenoptera: Braconidae, Aphidiinae). Colonies in which natural enemies were observed were on average larger than those without natural enemies (*M. fuscoviride*: 153 ± 11 vs. 112 ± 5 aphids, $t = -3.5$, d.f. = 551, $P < 0.001$; *M. tanacetaria*: 25 ± 1 vs. 16 ± 1 aphids, $U = 94417$, $N = 1304$, $P < 0.001$).

Due to the low number of natural enemies encountered, the observational data suggest natural enemies as possible causes of extinctions in less than 10% of all extinctions (Table 2). Host plant death was responsible for colony extinction in roughly one fifth (*M. fuscoviride*) and one quarter (*M. tanacetaria*) of cases (Table 2). Dispersal by winged morphs and competitive exclusion by the other aphid species are unlikely to be significant causes for the disappearance of colonies in tansy aphids (Table 2).

Discussion

Insect herbivores that feed on annual or bi-annual plants with frequent extinctions of local

Table 2. Number (percentage) of aphid colonies for which there was observational evidence of the involvement of particular factors in colony extinction (initially colonised islands only).

Suspected cause of extinction/evidence	Observation	<i>M. fuscoviride</i>	<i>M. tanacetaria</i>
Predation			
(Presence of natural enemies in colony)	Week of extinction		
	Mites	0 (0.0%)	0 (0.0%)
	Predators	1 (0.1%)	8 (0.6%)
	Parasitoids	18 (3.3%)	19 (1.6%)
	Total	19 (3.4%)	27 (2.2%)
	Week before extinction		
	Mites	16 (2.9%)	115 (8.8%)
	Predators	17 (3.1%)	21 (1.6%)
	Parasitoids	13 (2.4%)	38 (2.9%)
	Total	46 (8.4%)	174 (13.3%)
Dispersal			
(Presence of winged morphs in colony)	Week before extinction	50 (9.0%)	220 (16.9%)
Competitive exclusion			
(Presence of other species in colony)	Week before extinction	4 (0.7%)	5 (0.4%)
Host plant death			
(Number of colonies on dead ramets)	Week of extinction	102 (18.4%)	300 (23.0%)
Total number colonies		553 (100%)	1304 (100%)

host populations necessarily show high population turnover (van der Meijden *et al.* 1992, Halley & Dempster 1996). In contrast, for insect herbivores feeding on perennial plants with a patchy distribution, extinctions of local populations may or may not be frequent (Harrison 1991, Harrison & Taylor 1997, Eber 2001). In fact, if one only considers perennial plants under 'natural' conditions, i.e. no fragmentation due to human influence, the number of described insect metapopulations is still relatively small, with most examples coming from butterflies (cf. Roslin 2000). The results of our field study in the Tvärminne archipelago show that both aphid species feeding on tansy, *M. fuscoviride* and *M. tanacetaria*, have high rates of turnover at all spatial scales investigated. At the scales of the ramet and genet, aphids persisted on average for only a few weeks, a time scale similar to what was observed in more disturbed habitats in Switzerland and Germany (Weisser 2000, Massonnet *et al.* 2002). In Tvärminne, survival at the level of ramets was slightly longer for the ant-tended *M. fuscoviride* than for the untended *M. tanacetaria*, but survival at the level of genets was not significantly different between the species. At the levels of plant groups and islands, persistence times were longer than on ramets and genets, but still on average shorter than the length of the season. As a consequence, on many islands, aphids did not persist long enough to produce diapausing eggs. Thus, at the level of the island as well as at the lower spatial levels, extinctions were common, pointing to the importance of dispersal and colonisations for the longer-term persistence of both species. In both *M. fuscoviride* and *M. tanacetaria*, colonisations and extinctions occurred throughout the season, at all spatial levels. Even though colonisations and extinctions peaked at different points in time for the different spatial levels and aphid species (Figs. 7 and 8), the occurrence of extinctions early in the season, and of colonisations late in the season, demonstrate the dynamic nature of the host-aphid system. These high rates of turnover are not apparent from the mean occupancy rates (Fig. 3) or the average numbers of individuals present in colonies or islands (Figs. 4 and 5) and emphasize that it is necessary to individually mark ramets and genets to unravel the short-

term persistence of aphids at the different spatial levels. Taken together, the data suggest that there is no long-term persistence of aphids at any of the spatial levels investigated. Hence, in both species, long-term persistence must be attributed to population processes occurring at an even higher spatial level such as the Tvärminne archipelago.

In Tvärminne, the life-cycle of both aphid species is significantly shorter than in mainland Europe, where aphids hatch in April and where sexual morphs are not observed before the end of September (Weisser 2000). In both aphid species, dispersal by winged asexual females was confined to the first half of the season. This implies that in Tvärminne, at least at the level of islands and plant groups, no new populations are founded after mid-August, and that colonisations thus stop well before the end of the season. Within plant groups, and in particular within genets, there is still dispersal by wingless morphs, from one ramet to another, and from one genet to another, but the wingless morphs are unable to colonise plants that are further away. Even though the 5-m criterion used to differentiate one plant group from another is somewhat arbitrary, we did not observe any colonisation of genets by wingless morphs unless the newly colonised plant was in the immediate vicinity of an already occupied genet. In fact, no group or island was newly colonised after week nine, when no more winged females were observed in the aphid colonies. Thus, the seasonal cycle of both species is characterised by two phases. During the first half of the season, populations expand due to population growth and the incidence of the species increase through colonisations of islands, groups, genets and ramets by winged individuals, and of genets and ramets by wingless morphs. In the second half of the season, there is a retraction phase when occupancy of islands and groups goes down but colonisations of ramets and genets by wingless individuals still takes place.

The short persistence times at the level of ramets are partly due to the die-off of plants (Table 2). However, plant death is not an explanation for the majority of colony extinctions, because many colonies went extinct before the ramet died. While there is the possibility that

plant induced defence responses limited aphid population growth (Karban & Baldwin 1997, Haukioja 2005), experiments where predators are excluded show that aphid populations of both *M. fuscoviride* and *M. tanacetaria* can grow and persist for many generations on tansy ramets (Stadler 2004, W. W. Weisser unpubl. data). There is evidence for competition among *M. fuscoviride* and *M. tanacetaria* as both species feed at the top of shoots (Fischer *et al.* 2001, Stadler 2004), but because occupancy at the level of ramets was generally very low with less than 5% of ramets occupied at any one time of the season (Fig. 3), there were very few cases where both aphid species colonised the same ramet. Indirect effects such as habitat selection to avoid competition, or through joint natural enemies can, however, not be excluded (cf. Morris *et al.* 2005). Emigration of all individuals from a plant regularly occurs in host-alternating aphid species that switch between, for example, trees and herbaceous plants at the beginning and the end of the season (Dixon 1985, 1998), but this does not occur in tansy aphids. The only likely cause for most colony extinctions is predation. Experiments in which predation is manipulated show that the persistence of aphid colonies is drastically reduced when predators are allowed to enter the colony (Frazer *et al.* 1981, Edson 1985, Dixon 1998, Minoretti & Weisser 2000, Stadler 2004). The evidence for the importance of predation from an observational study such as this one is, however, limited: the number of aphid natural enemies observed in aphid colonies was very low (Table 1), and in only a fraction of colony extinctions was there any observational evidence that predators were involved in colony extinction (Table 2). The reason for this might be that most predators only stay in aphid colonies for such a limited time that the chances of encountering them in action are very low (Minoretti & Weisser 2000). In addition, predators remove their prey from the colony such that there is no post-predation evidence that they were present in the colony. To quantify the proportion of extinctions in which natural enemies are involved requires an independent assessment of the frequency of predation events (cf. Östman *et al.* 2001).

At the level of a ramet, persistence times are limited by the persistence of the ramet, which

dies at the end of the season. Without predation, aphids can go through up to ten generations within a season given temperature fluctuations in the field (W. W. Weisser unpubl. data). At the level of the genet, persistence is theoretically possible for many years as tansy is a perennial plant. Even though the rate of extinction was very high at the level of a genet, there were plants on which aphids persisted from the beginning to the end of the season, and in which eggs were laid. Breeding in tansy aphids takes place at the level of individual colonies where males and females meet. There will be some exchange of sexual individuals among ramets within the same genet, and dispersal of winged males in *M. tanacetaria* to other genets, but the extent of these movements is as yet unknown. Because of the die-off of all ramets at the end of the year, individuals hatching from the eggs laid on a particular genet will mix in the following spring when they colonise the new ramets of the same genet. The level of the genets is therefore the smallest spatial scale at which long-lasting populations could and sometimes do form. Thus, while a balance of extinctions and colonisations, the hallmark of a metapopulation (Hanski 1999, Hanski & Gaggiotti 2004) can only be achieved at a higher spatial level as the island, such as the Tvärminne archipelago, the dynamics within and between genets determine the population structure of both *M. fuscoviride* and *M. tanacetaria*.

A hierarchy of spatial structures has been found for a number of insect metapopulations (Hanski 1999, Doak 2000a, 2000b, Eber 2001, Hanski & Gaggiotti 2004, Tschardt & Brandl 2004). Despite the apparent generality of hierarchically structured populations, both metapopulation theory and empirical work have largely avoided analysing the importance of hierarchical structure for species persistence (Hanski 2000, Smith *et al.* 2003, Hanski & Gaggiotti 2004). Here, landscape ecology may provide an exception, but in this context there is generally little emphasis on population dynamics (e.g. Wu 1999, Baguette & Mennechez 2004). Our preliminary analysis suggests that the spatial structuring of aphid populations on tansy does not allow an easy discrimination of discrete populations at a particular spatial level that would form a metapopulation at the next higher spatial level.

Rather, the high turnover rates at all the spatial levels investigated suggest that while ‘the metapopulation’ occurs at the archipelago level with genets hosting the local breeding units, the intermediate spatial scales are an important component allowing the persistence of both species. Whether or not similar patterns are found in other herbivores that use perennial plants as a host remains to be investigated, but the aphid example discussed here underlines the importance of including spatial hierarchy into studies of plant–herbivore population dynamics.

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