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Habitat variation, mutualism and predation shape the spatio-temporal dynamics of tansy aphids

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Abstract. 1. Spatially distributed resources can lead to the formation of metapopulations, where individual subpopulations are often small and can experience frequent local extinction events followed by recolonisation. An example of terrestrial metapopulations are specialised phytophagous insects on their patchily distributed host plants.

2. The present study investigated the population dynamics of a specialised aphid (*Metopeurum fuscoviride*) on its patchily distributed host plant (*Tanacetum vulgare*) and associated community of mutualistic ants and predators in a small-scale field site. Furthermore, aphid habitat differences (plant size, C/N ratio, location and surrounding vegetation) were quantified, and seasonal timing and precipitation were considered.

3. Seasonal timing and precipitation both had effects on aphid colonisation, extinction events and aphid colony persistence. Towards the end of the season, and after higher precipitation, aphid colonisation events decreased and extinction events increased. Plant size and location as well as aphid within-field dispersal determined the spatio-temporal distribution of aphid colonies.

4. Mutualistic ants (*Lasius niger* and *Myrmica rubra*) increased the chance of establishment of aphid colonies. However, when *M. rubra* was tending, aphid colony persistence was reduced. Aphid persistence and extinction were dependent on aphid abundance, as a higher colony size reduced the probability of extinction by predation.

5. The results emphasise the importance of dispersal limitation, population growth and the presence of mutualists when studying the spatio-temporal dynamics of tansy aphids, particularly in a small-scale field site.

Key words. Colonisation, extinction, interaction, *Metopeurum fuscoviride*, mutualist, predator.

Introduction

Community ecology aims to understand how species abundances and patterns of distribution influence species interactions and coexistence. In natural systems, resources can be patchily distributed, and individuals of species often move between patches to exploit the maximal resource (Charnov, 1976). If dispersal is rare enough, such that the dynamics of the subpopulations in resource patches are largely independent, populations may exhibit metapopulation characteristics (Hanski, 1998). A metapopulation is described as a ‘population of unstable local populations’ (Hanski, 1998, based on the work by Levins, 1969). These local populations are often small, and local extinction is a common occurrence with only limited dispersal allowing for colonisations of empty patches. While in the classic metapopulation model all patches are identical, in reality patches may differ greatly in abiotic and biotic factors, including interactions with competitors, predators and parasitoids, which may greatly affect local population dynamics.

In terrestrial systems, patchily distributed host plants can be considered a local resource patch surrounded by a matrix of unsuitable habitat, particularly for specialised herbivores. The most studied terrestrial metapopulation system is that of the Glanville fritillary butterfly, where the butterflies exhibit strong host plant preference for oviposition (Hanski *et al.*, 1994). Another metapopulation model system comprises specialised aphids (Homoptera, Aphidoidea) on patchily distributed host

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plants (Addicott, 1978; Weisser, 2000; Loxdale *et al*., 2011). For example, the Asteraceae tansy (*Tanacetum vulgare* L.) is able to propagate by tussock-forming rhizome growth, leading to clusters of genetically identical shoots. These different clusters vary in size and can be easily distinguished in the field. Local aphid populations (colonies) are confined to a particular plant individual and generally show low persistence times with extinction driven by top-down interactions with natural enemies (Weisser, 2000). It is host to several specialised aphids such as *Metopeurum fuscoviride* Stroyan (Aphididae) that have been shown to exhibit metapopulation structuring, with aphid populations genetically structured more at the individual plant level than at the site level (Loxdale *et al*., 2011). Between sites, there is limited gene flow such that the different metapopulations are genetically differentiated (Loxdale *et al*., 2011). Further, winged offspring are predominantly produced only during generations three to four at the start of the season (Mehrparvar *et al*., 2013). While unwinged pea aphids are known to be able to walk over 10 m (Ben-Ari *et al*., 2015), dispersal by unwinged aphids between isolated host plants or host plant patches is only likely over short distances as it holds a higher risk, e.g. from desiccation or predation (Losey & Denno, 1998). This means that during the mid-season and late season, dispersal among different host plants is restricted, and probably contributes greatly to the within-site metapopulation structuring we see at the individual plant level. Despite many metapopulation or metacommunity studies focusing on landscape-scale sites as their subpopulations or subcommunities, plant–aphid systems such as the tansy one may, in fact, be structured at a smaller fine-scale level. Such a system allows for a more in-depth study on the factors driving metapopulation dynamics, including patch heterogeneity and the multitude of biotic interactions that are experienced by aphids in natural systems.

Many aphids, including *M. fuscoviride*, are tended by mutualistic ants that, in return for a honeydew reward, benefit the aphids by providing protection against natural enemies, including parasitoid wasps and fungal pathogens (El-Ziady & Kennedy, 1956; Way, 1963; Buckley, 1987, Völkl, 1992; Flatt & Weisser, 2000). For example, in a poplar tree system, obligate myrmecophilous aphids (*Chaitophorus populicola*) were limited to 21% of their potential habitat due to ant preference for host plants (Wimp & Whitham, 2001). This will have a knock-on effect for the rest of the ecological community and can strongly influence community dynamics. In an aphid metapopulation system, the presence of mutualistic ants may therefore be important for the colonisation of a previously empty patch by aphids and the subsequent persistence of the colony. While many studies focus on the role of particular factors in such systems (Weisser, 2000; Thies *et al*., 2005; Loeuille & Leibold, 2008; Jones *et al*., 2015), few studies consider different factors together (e.g. Wimp & Whitham, 2001).

Here we investigate the population dynamics of tansy aphids, their associated ant mutualists and natural enemies in a small-scale field site. We aim to determine whether successful colonisation of a patch by aphids, and subsequent colony persistence are enhanced by the presence of mutualistic ants and winged (dispersal-efficient) aphid morphs. Assuming a beneficial effect of mutualistic ants, we also expect ants to reduce the rate of aphid extinction through protection against natural enemies. Patch variation, via differential effects of plant size, location and nutritional quality are expected to mediate the effects of mutualist–aphid–natural enemy interactions.

To test this, we followed the seasonal dynamics of aphids, characterised by colonisation and extinction events, as well as colony persistence and peak population size on the level of the plant. By understanding the effects of these forces, we can begin to understand what factors are important for structuring the community of aphids, ants and natural enemies.

Material and methods

Model system

Tansy is an aromatic and perennial herbaceous plant that is indigenous to Eurasia (Mitich, 1992). It occurs along roadsides or rivers as well as on wastelands (Halliday & Tutin, 1989). Tansy is colonised by different, specialised aphid species. The most common one is *M. fuscoviride*, an obligate myrmecophilous aphid species that is commonly tended by ants such as *Lasius niger* L. or *Myrmica rubra* L. (Formicidae). *Metopeurum fuscoviride* is an autoecious aphid species that produces unwinged sexual morphs at the end of the season (October to November, Mehrparvar *et al*., 2013). Mated, sexual females lay eggs at the bottom of the plant, from which fundatrix individuals emerge and start new colonies in spring (April) the following year (Mehrparvar *et al*., 2013). *Metopeurum fuscoviride* is attacked by specialised parasitoids, in particular *Lysiphlebus hirticornis* Mackauer (Aphidiidae; Starý, 1966; Weisser, 2000) and common aphidophagous predators.

Field survey

The field survey was performed on a rectangular field of 1400 m^2 in southern Germany (N 48°25′1.51″; E 11°46′1.19″) from May to October 2014 (Figure S1). Tansy plants occurred throughout the field. All plants that could be clearly distinguished from one another (~80%) were marked and their GPS locations were noted (Fig. 1). Additional tansy plants occurred at a distance of about 15 m, and others (~20 plants) at a distance of 50 m. Larger tansy patches are further away, at a distance of about 2 km. This is not unusual for tansy, as it is a locally abundant but regionally rare plant (Massonnet & Weisser, 2004; Loxdale *et al*., 2011).

Plant and surrounding habitat characteristics

As tansy grows radially and forms elliptical or roundish patches, we used an ellipsoid approximation for calculating the patch area (A) and measured the longest and shortest diameters of each plant patch (formula in Figure S2), covering the maximum expansion of the plant (including leaves). This was done twice, once at the beginning (A_{t0}) and again at the end (A_{t1}) of the season. When tansy was flowering, the overall height of the plant was measured, from the soil surface to the tallest (free-standing) stem. By multiplying the mean area (A_{t0} and A_{t1}) by the height, we calculated the *volume* of each plant patch (formula in Figure S2). The plant C/N ratio was measured by taking samples from fully expanded leaves in the middle of the season. Samples were dried in a drying oven at 65 °C for 3 days and analysed using 1–2 g of powdery leaf tissue material in an automated CHNS-O Elemental Analyser (EuroEA3000, HEKAtech GmbH, Wegberg, Germany). We also calculated a measure for the *accessibility* of a tansy plant, based on the position of all other mapped tansy plants in the field site. The accessibility is defined as the proportion of a plant that is not surrounded by other tansy plants and ranges from 0° to 360°; a plant with an accessibility of 0° is completely surrounded by tansy plants (low accessibility) and a plant with an accessibility of 360° is not surrounded at all (high accessibility) (Figure S3). Therefore, a plant with a high accessibility could be more easily discovered by immigrating winged aphids, as fewer tansy plants are blocking the way. The percentage of area with short vegetation (grass and small herbs) 2 m around the whole plant (i.e. 4 m diameter circle with the middle of the plant as the centre) was used as a measure of *exposure*, with higher percentages representing more exposed tansy plants.

Aphid dynamics

Marked plants ($N = 178$) were followed weekly, from 6 May 2014, before aphids were present, until 4 September 2014 (calendar week 19–36; 7 ± 2 day intervals). From then on, surveys were done every second week until 31 October 2014 (calendar week 44; 15 ± 2 day intervals), when aphids were no longer observed. The sampling order in each week was changed randomly. Between 09.00 and 17.00 hours, all stems of marked plants were carefully examined without disturbing the invertebrate communities. For each plant, *M. fuscoviride* aphid abundance was counted using a mechanical counter, distinguishing between winged and unwinged aphids, and the number of occupied shoots. A plant was defined as occupied if a single aphid was found on that plant. A colonisation event was defined as the first week of the appearance of aphids on a plant. An extinction event was assumed if no aphid could be found on the same plant in two consecutive weeks. A recolonisation (new colonisation event on a plant that was previously occupied by aphids) occurred if there were 2 weeks or more between aphid occupations. The persistence and the peak population size of colonies were calculated (a colony of aphids refers to the whole plant): persistence of aphids on a plant was defined as the number of weeks aphids were present during an uninterrupted occupation event, whereas the peak population size is the maximum number of aphids counted on a plant during an uninterrupted occupation event.

Ants and aphid natural enemies

The distance of each tansy plant to the nearest *L. niger* ant nest ($N = 62$) was measured (Fig. 1). For each marked plant the following variables were assessed weekly: ant species present and number of aphidophagous predators, identified to family level for Coccinellidae (ladybirds), Chrysopidae (lacewings), Cantharidae (soldier beetles), Forficulidae (earwigs) and to order for Araneae (spiders). The abundance of mummies (hardened shell of the host aphid after successful parasitism by a parasitoid wasp), considering only new mummies in each week, was also assessed.

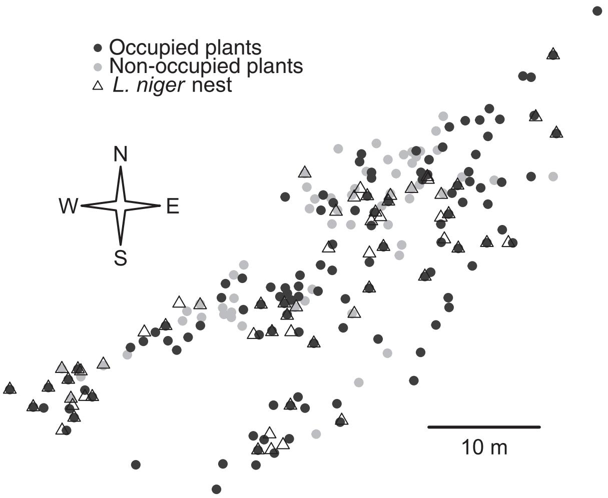

Fig. 1. Spatial distribution of *Tanacetum vulgare* plants occupied by *Metopeurum fuscoviride* aphids and *Lasius niger* ant nests. Unoccupied plants were randomly interspersed between occupied plants.

We calculated one predator– and mummy–aphid ratio for each occupied plant in each week. Furthermore, a proximity index was calculated for each plant based on the work of Gustafson and Parker (1992): the underlying idea of the index is that immigration of an organism is more likely if a potential source plant is closer to the focal plant, and if the number of individuals on the potential source plant is higher (see Figure S4). Proximity indices for aphids and for natural enemies, considering all winged predators (highly mobile), in particular ladybirds, soldier beetles and earwigs, were calculated. Less mobile predators such as lacewing larvae and spiders were excluded, due to a lack of robust data (i.e. low abundances) or their sessile foraging behaviour (web spiders).

Precipitation data were obtained from publicly available data of a weather station at N 48°24′32″, E 11°43′20″ provided by the Bavarian State Research Centre for Agriculture. This was used to calculate the cumulative amount of precipitation between two surveys.

Statistical analysis

Statistics and plots were carried out using R, version 3.1.1 (R Development Core Team, 2014) and the packages ‘effects’ (Fox, 2003; Fox & Hong, 2009), ‘lme4’ (Bates *et al.*, 2015), ‘sp’ (Pebesma & Bivand, 2005) and ‘vegan’ (Oksanen *et al.*, 2015). Variables used for modelling aphid dynamics are described in Table S1.

To analyse the spatial autocorrelation of aphid presence/absence summed over the whole season, a Mantel’s test with 9999 permutations using ‘manhattan’ distance matrices, for both presence/absence (1/0) and spatial distances between plants, was performed (Mantel, 1967). To test for the relationship between the number of colonisation events in each week and the abundance of winged aphids, a generalised linear model (GLM) with a quasi-Poisson error distribution was carried out. An association between the general aphid, ant and predator presence/absence throughout the whole season on each plant was tested using Fisher's exact tests.

Four different models were established to identify factors driving the seasonal dynamics of tansy aphids: colonisation and extinction events, as well as peak population sizes and persistence. As explanatory variables we included time, precipitation and a number of biotic factors, in particular plant traits (volume and C/N ratio), plant surrounding habitat characteristics (accessibility and exposure), aphid natural enemies (predator abundance/ratio and number/ratio of mummies) as well conspecifics on neighbouring plants and the interaction with third partners (presence/absence of mutualistic ants; Table S1). Model results were displayed using the 'effects' package in R, showing effects and their 95% confidence intervals of explanatory variables on response variables.

Colonisation model. The colonisation success of aphids for each plant in the weeks 21–32, comprising 96.8% of all colonisation events, was analysed using a maximum likelihood mixed regression approach. Only plants that were not occupied by aphids in the previous week were considered. Plants with a colonisation event and without a colonisation event in a particular week were used as a binary response variable (1/0) in a generalised linear mixed effect model fit (GLMER) with a binomial distribution and logistic link function. Explanatory variables were centred and scaled using the scale function in R to improve the interpretability of the results (Schielzeth, 2010). 'Plant' was used as a random effect in the model due to repeated measures on each plant to avoid pseudoreplication and 'week' was used within interaction terms to account for seasonal changes. A full model was fitted to the data and the backwards stepwise method used to remove nonsignificant terms. Minimal adequate models only are presented in the result section. Significance levels were calculated by using model comparison through likelihood ratio tests.

Extinction model. In each week, from week 21 to week 32, reflecting the main period in which 98.4% of all extinctions took place, plants that were occupied by aphids in the previous week were considered in the extinction analysis. Extinction events (plants no longer occupied) and non-extinction events (plant still occupied) were used as binary response variable (1/0) and analysed as described in the colonisation model. Additionally, the following interaction terms were used in the full model: aphid abundance × precipitation, aphid abundance × predator abundance, aphid abundance × mummies.

Peak population size model and persistence model. We tested the effect of the different factors on aphid peak population size and the persistence of aphid colonies on each plant (response variables: count data; one value per occupied plant, i.e. recolonisation events, were neglected). For plants with multiple colonisations over the season, only the values for the longest persistence time of aphids were considered. Data were analysed in a GLM with a quasi-Poisson error distribution (overdispersed data) and a log link function.

Additional GLMER models. GLMER models with a binomial distribution and logistic link function were used to explain a number of other further relationships: between the presence/absence of winged aphids during colonisation events and the proximity index of aphids, the week of colonisation as well as their interaction; between the presence of ants (not actually tending) and the distance to nearest ant nest. Plant and week were used as random effects. Significance levels were calculated by using model comparison through likelihood ratio tests.

Results

Aphids, ants and natural enemies

The first colonisations by *M. fuscoviride* aphids were observed in calendar week 20, mid-May (Fig. 2). In total, there were 125 colonisation events. Six of them were recolonisation events, i.e. colonisation following 2 weeks of no aphids. Thus, 119 out of 178 plants (66.8%) were occupied for at least 1 week. There was no spatial autocorrelation of aphid occupancy, i.e. plants that were never colonised ($N = 59$) were randomly interspersed between plants colonised by aphids ($N = 119$; Mantel's test, $r = -0.04$, $P = 0.983$; Fig. 1). The cumulative number of aphids counted was 32 093, of which 392 were winged individuals. The latter started to appear at the beginning of June. With an increasing number of winged individuals, the number of colonisation events also increased (GLM, $F_{1,20} = 74.77$, $P < 0.001$; Fig. 2). Following this, the number of occupied plants remained rather constant for 4 weeks, with a maximum of 81 plants (45.5%) in week 26 (late June), until week 28 (mid-July). Without any new colonisations and an increasing extinction rate with two peaks in weeks 27 and 30, the number of occupied plants dropped (Fig. 2). Three weeks after the last observation of winged individuals, in week 28, the last colonisation event occurred. Sexual morphs were encountered on only two plants which were still occupied in week 36 (early September). The last extinction event occurred in calendar week 44 (end of October; Fig. 2). Aphids were present on only one of the two plants with sexual morphs early in the season of the following year.

Four different ant species were encountered on tansy plants (Figure S5): *L. niger*, *M. rubra*, *Formica cunicularia* L. and *Formica fusca* L. However, only *L. niger* and *M. rubra* were observed tending *M. fuscoviride* aphids. Thus, the non-tending species (*F. cunicularia* and *F. fusca*) were combined for further analysis (*Formica* sp.).

In total, 877 ladybirds, 833 soldier beetles, 227 spiders, 97 earwigs and 13 lacewing larvae were observed on tansy plants. Ladybirds were more likely to be observed on plants where aphids occurred at some point during the season as opposed to plants never occupied by aphids (Fisher's exact test,

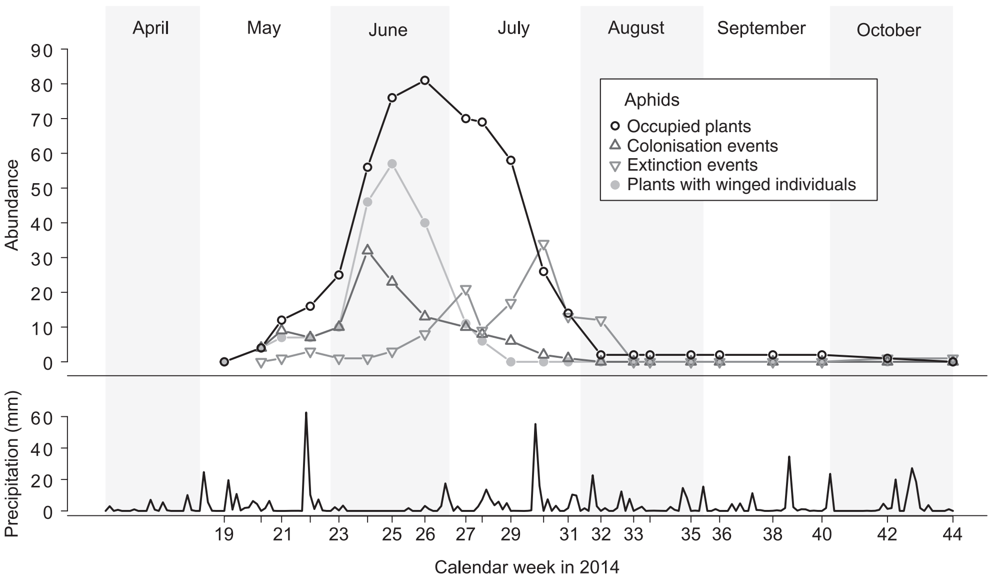

Fig. 2. Metapopulation structure of *Metopeurum fuscoviride* aphids and precipitation. Tick marks indicate the sampling in a particular week. Precipitation is shown on a daily basis. Survey in week 19, 6 May 2014; survey in week 44, 31 October 2014.

$N = 178$, $P = 0.004$), as were spiders ($P = 0.025$) and earwigs ($P = 0.002$); however, soldier beetles ($P = 0.148$) and lacewing larvae ($P = 0.342$) occurred with equal frequency on colonised and non-colonised plants (Figure S6). Over the season, 1025 mummies (parasitised aphids) occurred on 61 plants, first observed in week 23.

Aphid dynamics – colonisation events

Aphid dynamics within the field site followed a seasonal pattern (Fig. 2), with more plants colonised early in the season (week, $\chi^2_1 = 11.87$, $P < 0.001$; Table 1). Overall, the likelihood of colonisation decreased with increasing precipitation in the week before the colonisation event (precipitation, $\chi^2_1 = 19.02$, $P < 0.001$; Table 1), driven in particular by a dry spell between weeks 22 and 26 that coincided with the main aphid dispersal period (Fig. 2).

Colonisation by aphids was more likely on larger plants (volume, $\chi^2_1 = 16.35$, $P < 0.001$; Table 1) and, at the start of the season, on those with a higher accessibility, i.e. plants less surrounded by other tansy plants (week × accessibility, $\chi^2_1 = 8.53$, $P = 0.004$; Table 1; Fig. 3a). There was no effect of the exposure of tansy plants above surrounding vegetation or nutritional status of the plant in terms of C/N availability on aphid colonisation probability (Table 1). Towards the end of the season, aphids moved to less accessible plants (Fig. 3a). The probability of a plant being colonised was higher when they were closer to already occupied plants with a higher number of aphids, i.e. higher proximity index (aphid proximity, $\chi^2_1 = 8.18$, $P = 0.004$; Table 1; Fig. 3b). Interestingly, the aphid proximity index was higher on plants without winged individuals during colonisation ($N = 52$) than on plants where winged individuals were present at the time of first appearance of a colony ($N = 73$), suggesting colonisation by unwinged aphids at a very local scale (additional GLMER, $N_{\text{observations}} = 125$, $N_{\text{plants}} = 119$, $\chi^2_1 = 5.24$, $P = 0.022$; Fig. 3c). As the season progressed, the aphid proximity index increased for plants with and without winged individuals during a colonisation event ($\chi^2_1 = 9.40$, $P = 0.002$; Fig. 3c). However, no winged individuals were present during colonisation events at the end of the season (week 28 until week 31; Fig. 3c).The interaction term between aphid proximity index and time was not significant.

The presence of potentially tending ants on currently unoccupied plants increased the chance of a subsequent colonisation by aphids by 6% for *L. niger* ($\chi^2_1 = 12.89$, $P < 0.001$) and 4% for *M. rubra* ($\chi^2_1 = 3.78$, $P = 0.052$; Table 1; Fig. 3d). When other ant species, i.e. *F. cunicularia* or *F. fusca*, were present, the colonisation probability was lower and comparable to plants where none of the tending ants were present, and even decreased across the season (*Formica* sp., $\chi^2_1 = 5.01$, $P = 0.025$; and week × *Formica* sp., $\chi^2_1 = 5.00$, $P = 0.025$; Table 1). Despite these effects of ants on aphid colonisation, we found that ants were distributed across the whole site and not spatially limited to particular plants: all ant species (summed over the entire season, i.e. 1/0 for each plant) could be found equally among plants that were unoccupied and those that were once occupied by aphids (Fisher's exact test, $N = 178$, *L. niger*, $P = 0.093$; *M. rubra*, $P = 0.83$; *F. cunicularia*, $P = 0.51$; *F. fusca*, $P = 0.87$), although the presence of scouting *L. niger* ants on plants currently unoccupied by aphids was more likely if a *L. niger* nest was close by (additional GLMER, $N_{\text{observations}} = 1629$, $N_{\text{plants}} = 177$, $\chi^2_1 = 24.54$, $P < 0.001$).

Predator abundance had no effect on aphid colonisation (predator abundance, nonsignificant term; Table 1), but we found that a higher number of predators were in close proximity around newly colonised plants (higher proximity index) than around plants that were not colonised by aphids in a particular week (predator proximity, $\chi^2_1 = 5.82$, $P = 0.016$; Table 1). This was most apparent at the beginning of July during the main

Table 1. Effects on seasonal aphid dynamics and their performance.

	Colonisation model†				Extinction model†				Persistence model‡				Peak population size model‡			
	$N_{obs.} = 1629$; $N_{plants} = 177$; $N_{weeks} = 12$				$N_{obs.} = 507$; $N_{plants} = 119$; $N_{weeks} = 12$				$N_{plants} = 119$; Residual d.f. = 115				$N_{plants} = 119$; Residual d.f. = 114			
Response variable	d.f.	χ^2	*P*	Effect	d.f.	χ^2	*P*	Effect	d.f.	F	*P*	Effect	d.f.	F	*P*	Effect
Seasonal parameters																
Week	**1**	**11.87**	**<0.001**	↓	**1**	**44.76**	**<0.001**	↑	**1**	**113.45**	**<0.001**	↓	**1**	**70.54**	**<0.001**	↓
Precipitation	**1**	**19.02**	**<0.001**	↓	**1**	**16.70**	**<0.001**	↑	x	x	x	x	x	x	x	x
Plant traits																
Volume	**1**	**16.35**	**<0.001**	↑	**1**	**4.39**	**0.036**	↓	–	–	–	–	**1**	**7.49**	**0.007**	↑
C/N ratio	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plant surrounding habitat																
Accessibility	1	0.17	0.679	–	–	–	–	–	–	–	–	–	–	–	–	–
Exposure	–	–	–	–	1	0.04	0.840	–	–	–	–	–	–	–	–	–
Aphid abundance and migration																
Aphid abundance	x	x	x	x	**1**	**29.26**	**<0.001**	↓	**1**	**122.07**	**<0.001**	↑	x	x	x	x
Occupied stems	x	x	x	x	–	–	–	–	x	x	x	x	x	x	x	x
Aphid proximity	**1**	**8.18**	**0.004**	↑	**1**	**6.95**	**0.008**	↓	x	x	x	x	x	x	x	x
Mutualists																
Lasius niger	**1**	**12.89**	**<0.001**	↑	–	–	–	–	–	–	–	–	–	–	–	–
Myrmica rubra	1	3.78	0.052	↑	**1**	**4.49**	**0.034**	↑	**1**	**17.80**	**<0.001**	↓	–	–	–	–
Formica sp.	**1**	**5.01**	**0.025**	↓	–	–	–	–	–	–	–	–	**1**	**5.45**	**0.021**	↓
Predators and parasitoids																
Predator proximity	**1**	**5.82**	**0.016**	↑	–	–	–	–	x	x	x	x	x	x	x	x
Predator abundance	–	–	–	–	1	0.83	0.364	–	x	x	x	x	x	x	x	x
Predator-aphid ratio	x	x	x	x	x	x	x	x	–	–	–	–	**1**	**8.04**	**0.005**	↓
Mummy abundance	x	x	x	x	**1**	**21.26**	**<0.001**	↓	x	x	x	x	x	x	x	x
Mummy–aphid ratio	x	x	x	x	x	x	x	x	–	–	–	–	–	–	–	–
Interaction terms																
Week × exposure	–	–	–	–	**1**	**5.17**	**0.023**	↑	x	x	x	x	x	x	x	x
Week × accessibility	**1**	**8.53**	**0.004**	↓	–	–	–	–	x	x	x	x	x	x	x	x
Week × *M. rubra*	–	–	–	–	**1**	**4.44**	**0.035**	↑	x	x	x	x	x	x	x	x
Week × *Formica* sp.	**1**	**5.00**	**0.025**	↓	–	–	–	–	x	x	x	x	x	x	x	x
Week × proximity predators	**1**	**12.96**	**<0.001**	↓	–	–	–	–	x	x	x	x	x	x	x	x
Aphid abundance × predator abundance	x	x	x	x	**1**	**7.51**	**0.006**	↓	x	x	x	x	x	x	x	x

†Generalised linear mixed model fit by maximum likelihood with a binomial error distribution and plant as a random factor. Significance levels were calculated using model comparison through likelihood ratio tests. Interactions between all explanatory variables and week were tested. Interactions not listed were not retained in the final model. In the extinction model the following additional interactions were tested: predator abundance × aphid abundance × week; mummies × aphid abundance × week; and precipitation × aphid abundance × week.

‡Generalised linear model fit iteratively reweighted least squares with a quasi-Poisson error distribution.

Significant values are highlighted in bold type. '–' shows where a term was not retained in the most parsimonious model. 'x' shows terms that were not included in the model. ↑↓ indicates positive or negative effect on response variable. N_{obs}, number of observations; N_{plants}, number of plants; N_{weeks}, number of weeks considered for analysis.

Dynamics are characterised by colonisation and extinction events, aphid colony peak population size and persistence.

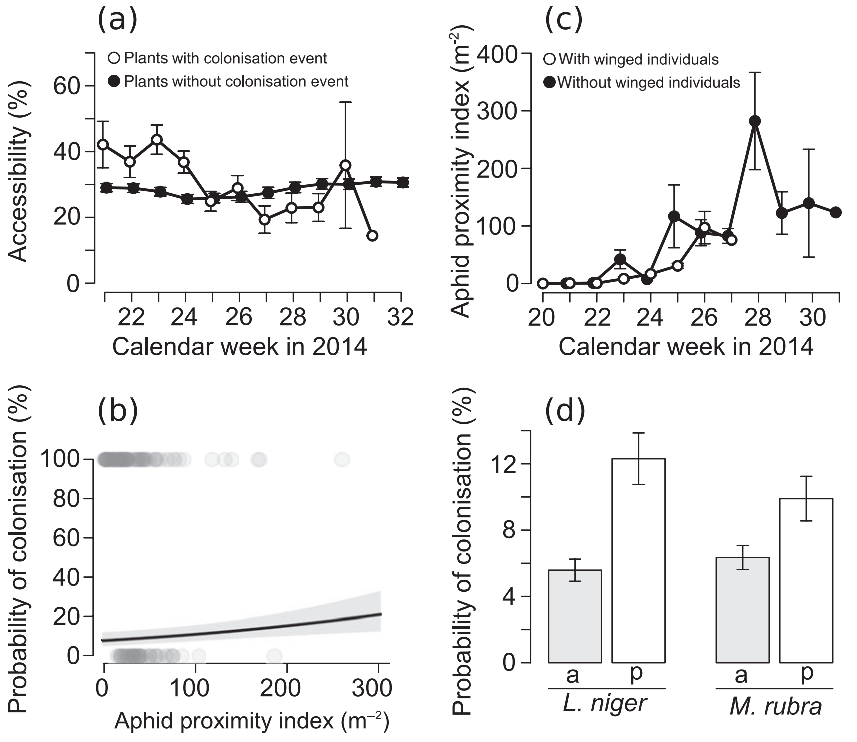

Fig. 3. Colonisation analysis. Accessibility, aphid proximity index and mutualistic ants. (a) Mean accessibility (±SE) of plants with and without an aphid colonisation event over the season. In each week only plants that were unoccupied by aphids in the previous week are considered. (b) Effect of aphid proximity index on colonisation probability, including 95% confidence interval based on the generalised linear mixed effect (GLMER) 'colonisation model' (Table 1). Points show individual values used in the model. (c) Mean proximity index (± SE), regarding the number of aphids on neighbouring plants in dependency of the presence/absence of winged aphids during colonisation events in each week. (d) Probability of colonisation events and presence (p) or absence (a) of potentially tending ants (*Lasius niger and Myrmica rubra*) in the previous week. Mean and SE calculated over all values, not accounting for plant as a random effect.

colonisation period (week × predator proximity, $\chi_1^2 = 12.96$, $P < 0.001$; Table 1).

Aphid dynamics – extinction events

The mean number of aphids on plants in the week before an extinction event was 27.4 ± 4.2 (mean ± SE), while the number of aphids on plants where no extinction occurred was 72.1 ± 5.3 (mean ± SE). Therefore, a higher total aphid population size on a plant reduced the probability of extinction (aphid abundance, $\chi_1^2 = 29.26$, $P < 0.001$; Table 1). Extinctions occurred more frequently later in the season (week, $\chi_1^2 = 44.76$, $P < 0.001$; Table 1). High precipitation in the week before also increased the chance of an extinction event (precipitation, $\chi_1^2 = 16.70$, $P < 0.001$; Table 1; Fig. 2). However, there was no significant interaction between aphid abundance and precipitation in our 'extinction model', i.e. small colonies were not more likely to suffer extinction due to precipitation (Table 1). Aphid colonies were less likely to become extinct on larger plants (volume, $\chi_1^2 = 4.39$, $P = 0.036$; Table 1), and also if nearby plants were still occupied by aphids at this local scale (aphid proximity, $\chi_1^2 = 6.95$, $P = 0.008$; Table 1). Aphids often colonised multiple stems of a plant, but the number of occupied stems did not alter the chances of becoming extinct at the plant level (Table 1), and neither did the plant nutritional status (C/N ratio) or plant accessibility (Table 1). The presence of *M. rubra*, however, increased the chance of becoming extinct (*M. rubra*, $\chi_1^2 = 4.49$, $P = 0.034$; and week × *M. rubra*, $\chi_1^2 = 4.44$, $P = 0.035$; Table 1), corresponding to the negative effect on colony persistence, but there was no beneficial effect of *L. niger* or *Formica* sp. ants (Table 1).

Towards the end of the season, aphid colonies on plants that were more exposed had a higher chance of getting extinct (week × exposure, $\chi_1^2 = 5.17$, $P = 0.023$, Table 1). The abundance of predators on a particular plant only influenced the chance of extinction dependent on aphid abundance, such that a higher predator abundance led to a higher chance of extinctions, but only if aphid abundance was low (aphid abundance × predator abundance, $\chi_1^2 = 7.51$, $P = 0.006$; Table 1; Fig. 4). Parasitoids did not contribute significantly to extinction events, in fact, mummies were found more frequently on plants where an extinction was less likely (mummies, $\chi_1^2 = 21.26$, $P < 0.001$; Table 1).

Aphid dynamics – persistence

Once on a plant, aphid colonies persisted for an average of 4.4 ± 0.3 (mean ± SE) weeks with a minimum of one and a maximum of 19 weeks. Colonies persisted longer if they were

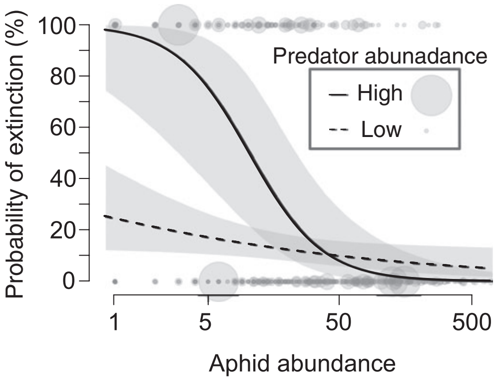

Fig. 4. Extinction analysis: predators and aphid abundance. Effects and their 95% confidence interval of the interaction between aphid abundance and predator abundance on extinction probability. Model estimates are based on either a ‘low’ or a ‘high’ predator abundance, corresponding to the minimum or maximum number of predators found on a single plant in the field, zero and 58 predators, respectively. Points show the individual values used in the extinction model and their sizes indicate the number of predators found on that particular plant. Point sizes also range from zero (‘low’) to 58 (‘high’) predators.

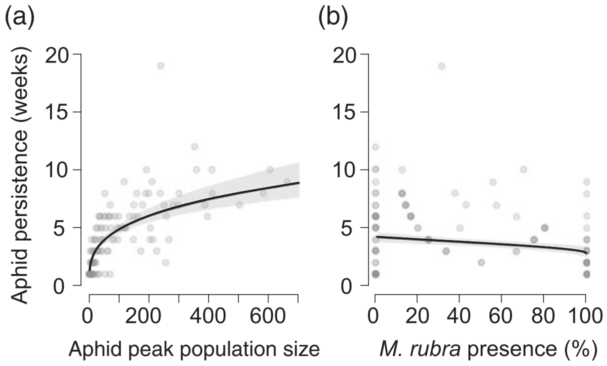

Fig. 5. Persistence, peak population size and mutualistic ants. (a) Persistence of aphid colonies depends on the aphid peak population size (maximum aphid abundance). The regression line shows the effect of aphid peak population size on persistence, including 95% confidence interval (CI). (b) Negative effect of presence of *Myrmica rubra* on aphid persistence, including 95% CI. The *x*-axis shows the percentage of weeks with ant presence during the time a plant was occupied by aphids.

established early in the season (week, $F_{1,117} = 113.45$, $P < 0.001$; Table 1) and built up a higher population size (aphid abundance, $F_{1,116} = 122.07$, $P < 0.001$; Table 1; Fig. 5a). Variation among host plants and the plant surrounding habitat (volume, C/N ratio, accessibility and exposure) did not contribute to differences in aphid colony persistence (Table 1). The only significant ant effect on aphid persistence was the presence of *M. rubra*, which reduced aphid persistence (*M. rubra*, $F_{1,115} = 17.80$, $P < 0.001$; Table 1; Fig. 5b).

We also found that neither the predator– nor the mummy–aphid ratio had a significant effect on the persistence of colonies (Table 1).

Aphid dynamics – peak population size

Aphid peak population sizes ranged between 1 and 662 (104.2 ± 12.2; mean ± SE). Higher numbers were reached when the colonies established early in the season (i.e. before mid-June; week, $F_{1,117} = 70.54$, $P < 0.001$; Table 1). In addition, a higher plant volume also supported higher peak population sizes (volume, $F_{1,116} = 7.49$, $P = 0.007$; Table 1). Tending ants did not affect the peak population sizes, whereas non-tending ants, i.e. *F. cunicularia* or *F. fusca*, had a negative effect (*Formica* sp., $F_{1,115} = 5.45$, $P = 0.021$; Table 1).

The predator–aphid ratio affected the aphid peak population size negatively, i.e. colonies with a higher predatory pressure had a lower peak population size (predator–aphid ratio, $F_{1,114} = 8.04$, $P = 0.005$; Table 1). The mummy–aphid ratio did not negatively affect aphid peak population sizes in our model (Table 1).

Discussion

We have shown that multiple interacting factors can drive aphid metapopulation dynamics in this tansy system. We found that more isolated plants were most likely to be colonised by winged individuals. However, colonisations also occurred in the absence of winged individuals, with unwinged aphids potentially dispersing very locally between closely located plants, especially late in the season. The proximity of a plant to other aphid-occupied plants affected both colonisations and extinctions, which suggests a possible influence of source–sink dynamics within our system (Utsumi *et al*., 2011).We were also able to show that plant size, the presence of mutualists and natural enemies drive aphid dynamics and that the strength of these effects varied across the season. Furthermore, aphid persistence and extinction were highly dependent on their abundance, as a higher colony size reduced the probability of extinction, e.g. resistance to extinction through predation.

Seasonal dynamics

At the start of the season, colonisation can occur as a result of the arrival of winged aphids either from other plants at the local scale or from other sites at the regional scale. The increase of winged aphids was associated with an increase in colonisation events, and was restricted to the short time-frame in which winged aphids are produced by this species (Mehrparvar *et al*., 2013). The earlier a plant became occupied, the longer aphids were able to persist on a particular plant. And while larger plants did benefit aphids, we found no effect of variation in C/N to explain this effect. Only two aphid colonies persisted past September to produce sexual morphs and hardy overwintering eggs, with a single plant contributing to the early founding population in the next season.

In our models, the amount of precipitation was associated with both a decreased chance of new colonisations and an increased chance of extinctions. However, the dry spell in June corresponded to the main dispersal event when winged offspring were produced, and therefore the link between low precipitation and more colonisations might just be a seasonal artefact. Thus, the effect of precipitation on extinctions and aphid abundance is more likely to have a causative nature. For instance, heavy rain is able to knock down grain aphids, *Sitobion avenae*, which then negatively affected the abundance of aphids, particularly if they do not survive to climb back up the plant (Mann *et al*., 1995).

Aphid dispersal

The scarcity of the production of sexual morphs at the end of the season indicates a sink population and points to the importance of regional scale dispersal, by winged aphids, at the start of the season (Fievet *et al*., 2007). This is also reflected by the within-field dispersal pattern that exhibited an immigration pattern, i.e. plants easily accessible (less blocked by surrounding tansy plants) were predominately occupied first (regional scale dispersal by winged aphids; Winder *et al*., 1999), potentially followed by local scale dispersal by unwinged aphids colonising plants within the field (surrounded by other tansy plants).

We tested the influence of dispersal limitations in our system by calculating a proximity index considering aphid colony sizes and their distance to the focal plant. We showed that plants that are closer to other plants with a higher number of aphids are more likely to become occupied (i.e. potential arrival of founders from neighbouring source plant) and already occupied plants are less likely to become extinct (i.e. arrival of rescuers: rescue effect; Gotelli, 1991). When there were no winged aphids present on newly occupied plants, they were in general closer to other occupied plants (higher proximity index). Hence, within-site dispersal by unwinged aphids moving from a plant with high performance (e.g. driven by phenotypic differences among plants; Clancy *et al.,* 2016) to a nearby plant with potentially lower performance could possibly contribute to the aphid metapopulation structure in this system (Utsumi *et al*., 2011). Zheng *et al*. (2009), for instance, were able to show that colonisation events by *M. fuscoviride* at the very local scale, i.e. within and between plants, are more likely to be caused by unwinged aphids due to their higher overall abundance. In other systems, unwinged morphs of the pea aphid, *Acyrthosiphon pisum*, are able to significantly contribute to within-field dispersal by walking distances of up to 13.5 m (Ben-Ari *et al*., 2015).

Alternatively, it is also possible that constantly immigrating winged aphids (i.e. from outside the field site) gradually colonise plant patches (i.e. less and less accessible plants and plants close to other occupied plants), especially as colonisation events coincided with the occurrence of winged individuals in the field site. The absence of winged individuals, then, could be explained by winged individuals moving to a plant, producing some offspring and then moving onto another plant further away. It is expected that a combination of all these explanations drives aphid dynamics, as winged aphid movement will predominantly have an influence during the main dispersal phase, whereas unwinged aphid movement can occur throughout the year. Here, further aphid genetic analysis could help to discriminate between different within-field dispersal patterns (e.g. Loxdale *et al*., 2011).

Variation in plant traits and plant surrounding habitat

Plant size and the plant surrounding habitat, in particular accessibility, influenced the spatio-temporal distribution of aphids (immigration and within-field dispersal). An increasing patch size offers a larger target, has a higher capacity and a lower extinction rate to prey species (Holyoak *et al*., 2005). In our system, plant size was indeed an important driver of aphid colonisation, with larger plants supporting higher peak population sizes and reducing the chance of extinctions. This could be explained by the fact that it is more likely for an aphid to discover a larger plant, but an alternative explanation would be variation in the nutritional suitability of the different plants. While this hypothesis is not supported by plant C/N ratio, such that basic plant stoichiometry was not driving these processes, there may be other nutritional or phenotypic differences among plants that we have not tested here, particularly as aphids feed on the plant phloem sap rather than the leaves themselves. Further, chemical variation in the tansy plants may also mediate some of the interactions we have shown here (Clancy *et al*., 2016). Larger plants are also potentially less affected by environmental stressors, e.g. water stress or surrounding vegetation, as interspecific competition is one of the main biotic stressors for plants (Takabayashi *et al*., 1994; Boege, 2010). This could lead to a lower stress level and therefore a lower *a priori* resistance to aphids.

Mutualists

It is emphasised that environmental factors, intraspecific interactions as well as, to some extent, interspecific interactions, alongside spatio-temporal factors, are important drivers of community dynamics (Leibold *et al*., 2004; Holyoak *et al*., 2005, Mutshinda *et al*., 2009). Predominantly the focus of this has been on competitive models with a competition–colonisation trade-off or predator–prey interactions (e.g. Hastings, 1980; Tilman, 1994; Weisser, 2000; Winder *et al*., 2001; Leibold *et al*., 2004; Pillai *et al*., 2012), but we show that mutualists can also drive changes in aphid metapopulation structure. The fitness of obligate myrmecophilous aphids is strongly increased through associations with mutualistic ants (Stadler *et al*., 2002; Stadler & Dixon, 2005).

Although tansy plants offer no extrafloral nectaries and flowers (i.e. floral nectaries) were not present in the early and mid-season, ants were present on currently unoccupied tansy plants. Ants were never observed showing explicit feeding or hunting behaviour on tansy (M. Senft, pers. obs.) or tending other aphid species. Ants were patrolling or scouting the plants, potentially waiting for aphids to arrive. The presence of ants on tansy plants, before aphid colonisation, was recently shown to vary across different plant chemotypes, suggesting they are attracted or repelled by certain chemical compounds emitted by the plant (Clancy *et al*., 2016). Thus, it is not surprising that the presence of potentially tending ants increased the chance of subsequent aphid colonisation of that plant, as an aphid on a plant more often patrolled by mutualistic ants can be discovered faster. It should be advantageous for these aphids to be encountered by mutualistic ants as quickly as possible, because ants can decrease predation pressure, promote aphid development and increase fecundity (reviewed in Stadler *et al*., 2001). Ants are known to inhibit aphid dispersal by physically removing wings or through chemical manipulation (Oliver *et al*., 2007). Thus, the immediate presence or absence of ants could define whether or not a plant is successfully colonised. However, an obligate myrmecophilous aphid species, as in our system, might also be able to actively choose plants where potentially tending ants are present, as shown for other herbivores that respond to ant cues (Gonthier, 2012). A further alternative is variation in honeydew – ants and aphids try to colonise all plants, but ants only tend aphids on certain plants that provide high-quality honeydew (Fischer & Shingleton, 2001; Stadler *et al*., 2002; Vantaux *et al*., 2011).

Ant presence (*L. niger* workers on currently unoccupied plants) was more likely when a nest was nearby. However, as ants were not spatially limited to certain plants, this is probably a temporal effect (increased visiting frequency) which, in turn, affected the colonisation probability of aphids. A similar pattern has been shown for other myrmecophilous aphid species where aphid abundance declined with increasing distance to ant nests, and therefore aphids were only able to use a fraction of their potential habitats (e.g. Wimp & Whitham, 2001; Fischer *et al*., 2015). The presence of different ant species on a particular patch could have dramatic effects on other members of the community, particularly as we found that *M. rubra* had a negative effect on aphid colony persistence. Such an effect could have occurred through predation, disturbance (e.g. interspecies competition; Binz *et al*., 2014), higher fitness costs for tending ants and therefore a lower willingness to defend against aphid natural enemies (reviewed in Stadler & Dixon, 2005). Furthermore, it is also possible that these ants change their mutualistic behaviour to an antagonistic behaviour and act as predators after a few weeks of tending, leading to a higher probability that colonies will become extinct. This might also be true for ants never observed tending aphids on this field site (*F. cunicularia* and *F. fusca*), which would also explain the lower aphid peak population size and colonisation probability observed in our data when these ants were present.

Predators

The density of predators around newly colonised plants was significantly higher than on plants that did not become occupied. Aphidophagous predators often accumulate in areas where prey density is high to ensure a continuing food availability, and also as part of their ovipositioning strategy (Dixon, 1959; Hemptinne *et al*., 1992).

As shown in numerous predator exclusion experiments, specialised predators (e.g. parasitic wasps) are most effective in reducing aphid populations (Diehl *et al*., 2013). However, in the field, it has never been proved that aphidophagous predators such as ladybirds can effectively control aphid populations, as they do not have a consistently negative effect on the maximum number of aphids (generation time ratio hypothesis; Kindlmann & Dixon, 1999; Kindlmann *et al*., 2015). Additionally, the effect of aphidophagous predators can also be reduced due to the protective service offered by mutualistic ants (e.g. El-Ziady & Kennedy, 1956). In our system, we found that aphid colonies that suffered a higher predation pressure (i.e. higher predator–prey ratio) had a lower peak population size. However, predators in our system were only able to drive a colony to extinction when the abundance of aphids was already low (colonies with a higher number of aphids could withstand multiple attacks of predators and therefore persist longer). Such a low aphid abundance could arise from repeated predation visits (Meyhöfer, 2001), evident from our model, but also from a low performance of a colony on certain plants (Zytynska & Preziosi, 2011) or due to suboptimal ant protection (reviewed in Way, 1963), as well as from high emigration (Karley *et al*., 2004) and low immigration (Carter & Dixon, 1981).

In contrast to Weisser (2000), where aphid extinctions were mainly driven by a parasitoid, we found that aphid mummies could be found on plants where colony extinction was less likely. This seems plausible, because it would guarantee a higher chance of survival for the parasitoid itself, especially when that colony is benefiting from ant protection (Völkl, 1992). This could occur through increased survival chance of a parasitoid larva when ants are tending the aphid (e.g. reduced risk of fungal infection) and lower per-capita risk of predation or hyperparasitism in a large colony. Nevertheless, parasitised conspecifics could also be advantageous for the non-parasitised aphids themselves: Fievet *et al*. (2009) found that aphids reduce emigration from patches with higher number of mummies, as the presence of the latter reduces further parasitoid pressure. Therefore, parasitoids could affect the dynamics in our system by reducing dispersal from such patches. However, this remains speculation, as we did not test that directly.

Aphid metapopulation dynamics

Previous work has shown that our focal aphid shows a metapopulation structure with aphids on a single plant forming a local population (Weisser, 2000; Loxdale *et al*., 2011). Due to the different spatial limitations by the species in this community (aphids, mutualists and predators, ranging from high to low), this system does not fit into classical metacommunity framework, where interacting species optimally exhibit a similar limited dispersal pattern and patch boundaries are more distinct (Leibold *et al*., 2004). However, these species are still interacting and influencing the metapopulation of these aphids, although the different species act on different spatial scales: one novel finding, for instance, is the role of mutualistic ants in shaping the metapopulation structure in this system, especially during establishment of new aphid colonies. To our knowledge this is the first study showing such an effect of ants on the colonisation success of aphids. Furthermore, top-down predation effects do not exclusively drive aphid metapopulation structuring in this system as previously thought (Weisser, 2000).

In fact, a combination of many factors work together to determine the community structure on tansy. We were, for instance, also able to show that mass effects potentially drive metapopulation dynamics in our system, as migration from source to sink patches not only promoted colonisation of other plant patches, but also rescued plants from becoming extinct (rescue effect). Thus, metapopulations must be considered in the context of the community in which they live.

While metacommunity ecology research is still relatively theoretical, there is an increasing number of empirical studies, particularly within aquatic ecosystems where interacting species inhabit different ponds and thus are similarly limited in their dispersal (Logue *et al*., 2011). Simply scaling up from a metapopulation to a metacommunity is difficult in natural terrestrial systems due to the mismatch of home-range sizes and/or dispersal ability (Leibold & Miller, 2004). However, we suggest that plant–insect systems are particularly useful in studying the underlying mechanisms driving metacommunity processes in terrestrial systems (see also van Nouhuys & Hanski, 2005; Zheng *et al*., 2015). Specialised insects feeding on patchily distributed hosts, such as the tansy system, offer many advantages over other systems to investigate these dynamics, especially at a fine scale. We can learn much from the mechanisms underlying metacommunity dynamics, to further understand the processes important in spatially structured habitats that may not fall under the classic idea of a metacommunity.

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Conflict of interest: The authors declare that they have no conflict of interest.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Figure S1. Picture of the field site in Altenhausen, north of Freising in southern Germany.

Figure S2. Calculation formulae for the plant volume.

Figure S3. Illustration and calculation of the accessibility of a plant.

Figure S4. Formula to calculate the proximity index.

Figure S5. Weekly percentage of occupied and unoccupied plants on which a particular ant species occurred.

Figure S6. Number of plants with and without aphids on which a particular predatory species occurred.

Table S1. Variables and their characteristics used for modelling aphid dynamics.

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