Ilkka Hanski: The legacy of a multifaceted ecologist

The roles of trophic interactions, competition and landscape in determining metacommunity structure of a seed-feeding weevil and its parasitoids

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Community composition is determined by attributes of the environment, individual species, and interactions among species. We studied the distributions of a seed weevil and its parasitoid and hyperparasitoid wasps in a fragmented landscape. The occurrence of the weevil was independent of the measured attributes of the landscape (patch connectivity and resource availability). However, between habitat-patch networks, weevil density decreased with increasing parasitism, suggesting top-down control, especially in the north. Parasitism was mostly due to a specialist and a generalist that appeared to compete strongly. This competitive interaction was strongest at high patch-connectivity, perhaps due to a trade-off of local competitive ability and dispersal. Finally, the abundance of the generalist hyperparasitoid was unrelated to landscape or host-species abundance. The snapshot presented by these data can best be explained by top-down effects, interactions among species, host ranges, and patch configuration in the landscape, but not by local host-plant abundance.

Introduction

Communities are made up of species living in a shared habitat. Which species are present, their abundances and the complexity of the food web can depend on attributes of the habitat and the surrounding landscape. Many species in a community also interact so their persistence and prevalences are interdependent. This is especially true for strongly interacting species such as those competing for a shared resource, or those in predator–prey relationships (Cornell & Lawton 1992). Finally, when species inhabiting a

landscape are considered a metacommunity, then the spatial structure and heterogeneity of the landscape can contribute to the complexity of the metacommunity (Holt 2002, Amarasekare 2008). To understand the structure of a community, as well as its dynamics and resilience, we must determine the roles of both spatial factors and biotic interactions (Leibold *et al.* 2004). This is most tractable for species with narrow resource requirements and strong interactions with other species (van Nouhuys & Hanski 2005).

A community made up of host plants, their insect herbivores, parasitoids and hyperparasit-

oids provides such a scenario. There are several studies of plant–herbivore–parasitoid communities that highlight specific attributes of the system in determining the species abundances, such as local plant density (Hambäck & Englund 2005), host-plant quality (Price & Hunter 2015, Riolo *et al*. 2015), and higher trophic level interactions (Cronin 2007). Only a handful of studies were on a scale appropriate to address the role of spatial configuration of the habitat in determining community or metacommunity structure (e.g. Amarasekare 2000, Harrison *et al*. 2005, Laszlo & Tothmeresz 2013, Cronin & Reeve 2014, Riolo *et al*. 2015). Both landscape structure and local species interactions are clearly important in determining the composition and dynamics of some communities, such as the Glanville fritillary butterfly and its parasitoids and hyperparasitoids in the Åland Islands, Finland (van Nouhuys & Hanski 2005). But the relative importance of these intrinsic and extrinsic factors must vary depending on attributes of the landscape such as structure and primary productivity; attributes of the species such as resource breadth, mobility, and size; as well as food web complexity, and the spatial scale of the study.

The monophagous weevil *Mecinus pascuorum* (Coleoptera: Curculionidae) feeds on the developing seeds of *Plantago lanceolata* (Plantaginaceae). In the Åland Islands, the weevil is part of the community of herbivores inhabiting *P. lanceolata* in dry meadows, pastures and disturbed areas, where it is host to a community of parasitoids (Vikberg & Nieminen 2012, Nieminen & Vikberg 2015). The meadows are characterized as the setting for the long-term study of the metapopulation biology of the Glanville fritillary butterfly *Melitaea cinxia* (Lepidoptera: Nymphalidae) (Nieminen *et al*. 2004, Hanski 2011, Ojanen *et al*. 2013, Fountain *et al*. 2016) and its parasitoids (Lei *et al*. 1997, van Nouhuys & Hanski 2005, Nair *et al*. 2016).

We studied the association of environmental factors and species interactions, with the abundance of the weevil *M. pascuorum* and its associated parasitoids, using a sample of 6170 individuals collected from 18 patch networks in the Åland Islands in 2009. These data are described in Nieminen and Vikberg (2015). The environmental factors were latitude, patch connectivity in the landscape and local host plant abundance. The species interactions were rates of parasitism and hyperparasitism. Out of the many possible outcomes, we expected that the weevil abundance would be positively associated with the local *P. lanceolata* abundance due to resource concentration in terms of apparency (Root 1973) and availability (Rand *et al*. 2014), and that weevil abundance would also increase with habitat patch connectivity because highly connected patches provide a large stable resource over time (Hanski 1998). The same argument can be made for the parasitoids, in which case we would expect a high rate of parasitism where the plant and host weevil are abundant. On the other hand, parasitoids can cause host population size to decrease, which would diminish the association of weevil population size with plant abundance (Jones *et al*. 1994, Walker *et al*. 2008), and could increase the association of patch connectivity with host and parasitoid population sizes (Hassell 2000). We would also expect competing parasitoids to be negatively associated (Hassell & Waage 1984), and to have contrasting distributions in the landscape if, for example, there is a trade-off between dispersal ability and local competitive ability (Calcagno *et al*. 2006). Going up one trophic level, we expected hyperparasitoids to influence the overall rate of parasitism and the competitive relationship between host parasitoids (Sullivan & Völkl 1999, van Nouhuys & Hanski 2000), the effects of which can depend on landscape connectivity (Holt & Hoopes 2005). Lastly, we expected the interactions among species to be weaker with wider resource breadth or host range (van Nouhuys 2005). These types of patterns are predicted theoretically, and are important to understanding biodiversity as well as biological control of insect pests (Holt 2002, Frago 2016, Kaser & Ode 2016). There are many empirical examples of subsets of them but they are seldom addressed simultaneously on a large scale in a natural system.

Material and methods

Study species

Mecinus pascuorum is a monophagous seed-

feeder of *P. lanceolata*. Females lay one egg per developing seed capsule, each larva usually consumes two seed capsules, and pupation takes place within the seed capsule (Dickason 1968, Mohd Norowi *et al*. 1999). In the Åland Islands, adult emergence peaks around early August. They overwinter as adults, and are most active in late May and June (Nieminen & Vikberg 2015).

Mesopolobus incultus (Hymenoptera: Pteromalidae) is a solitary primary parasitoid of *M. pascuorum* (e.g. Norowi *et al*. 2000). It is apparently a specialist on *M. pascuorum* in the Åland Islands, though there are records of other host weevils as well as *Apion* species feeding on *Trifolium* (*see* e.g. Baur *et al*. 2007). For further discussion *see* Nieminen and Vikberg (2015).

Eupelmus vesicularis (Hymenoptera: Eupelmidae) is a highly generalist species that, according the literature acts as both a primary and a secondary parasitoid (Gibson 1995, Noyes 2013). Females are brachypterous which limits their dispersal ability, but Gibson (1995) suggests that on a local scale the wasp is a superior competitor over other parasitoid species due to its wide host range that includes primary parasitoids as hosts. *Eupelmus vesicularis* has been presumed to attack both *M. incultus* and *M. pascuorum*, but *see* the section 'Comparison of *Mesopolobus incultus* and *Eupelmus vesicularis* adults' below.

Baryscapus endemus (Hymenoptera: Eulophidae) is a hyperparasitoid (Graham 1991) which attacks parasitoid wasps from the family Pteromalidae (Noyes 2013). In this community, it is highly likely to be a parasitoid of *M. incultus* but not *E. vesicularis* (Nieminen & Vikberg 2015).

Landscape, sampling and rearing

We studied factors determining metacommunity structure of the seed-feeding weevil *M. pascuorum* and its associated parasitoids by systematically collecting naturally infested *P. lanceolata* seed spikes from habitat patches in a well characterized landscape in the Åland Islands, Finland. We kept the spikes under laboratory conditions until weevils and parasitoids emerged and then analyzed the occurrence of the species with respect to each other, and to the configuration of

the habitat in the landscape. The habitat patches are open meadows, pastures and disturbed areas where *P. lanceolata* grows. In total, we sampled 643 habitat patches (size range 0.002–5.5 ha; *see* Table 1) between 29 July and 8 August 2009. *Plantago lanceolata* patches are naturally clustered in the landscape. These clusters were delineated into semi-independent patch networks (SINs) using the software SPOMSIM (Moilanen 2004). The number of patches, their areas and distribution differed among SINs; for thorough descriptions of the study sites *see* Nieminen *et al*. (2004) and Ojanen *et al*. (2013). We collected samples from each patch in 18 SINs spread over the Åland Islands (Fig. 1). The landscape structure was characterized based on the population biology of the butterfly *M. cinxia*. However, it is relevant for any species dependent on *P. lanceolata*. For instance, the dynamics and evolution of the phytopathogen *Podosphaera plantaginis* that infects *P. lanceolata* are in part determined by the same spatial landscape structure (Laine & Hanski 2006).

We collected *P. lanceolata* spikes from all parts of each patch. The number of spikes sampled from each patch was proportional to the abundance of *P. lanceolata* in it. Each spike was collected from a different plant. When the number of spikes in a patch was very low, we collected at most 10% of them. This procedure resulted in a sample of 1–161 spikes per patch (30.7 on average). We aimed to collect spikes with ripe seeds only. Spikes were placed individually in plastic tubes in the laboratory, and emerged insect individuals were transferred into coded Eppendorf tubes after about a month for identification by experts. Mortality during rearing was not scored, but based on our earlier experience it was likely low and unbiased due to uniform laboratory conditions. Details of sampling and rearing can be found in Nieminen and Vikberg (2015).

Comparison of *Mesopolobus incultus* and *Eupelmus vesicularis* adults

We compared the sizes of adult *M. incultus* and *E. vesicularis* wasps to infer whether the latter species might have been a primary parasitoid of

Table 1. Summary of the characteristics of the patch networks.

SIN	Current no. of patches	No. of patches sampled	No. of spikes sampled	Corrected no. of spikes in occupied patches	Total habitat area (ha)	Mean connectivity	Sum of PL coverage (m²) in 2008	No. of patches occupied by *M. pascuorum*	No. of *M. pascuorum* reared	No. of *M. incultus* reared	No. of *E. vesicularis* reared	No. of *B. endemus* reared	Rate of parasitism of *M. pascuorum*
2	21	20	369	332	0.38	0.15	NA	15	109	189	121	4	0.74
9	112	43	662	27	25.9	4.85	315.5	2	6	13	1	3	0.74
11	73	64	1546	1121	12.3	3.38	148.5	41	124	402	156	18	0.82
27	11	8	139	149	2.31	0.88	46.0	4	13	55	5	1	0.82
36	61	53	1616	1321	6.10	2.97	244.8	33	121	357	181	21	0.82
37	83	30	814	808	12.3	3.25	255.6	26	266	784	446	142	0.84
40	89	70	1780	189	19.0	5.22	348.6	6	3	22	4	1	0.90
47	39	33	546	300	5.85	1.67	48.0	13	26	73	37	4	0.81
50	172	109	5565	690	39.8	8.17	3308.6	8	8	29	5	1	0.81
57	68	57	1103	1045	10.8	3.65	213.9	39	275	688	103	59	0.76
63	19	14	194	243	2.01	0.62	14.5	0	0	0	0	0	NA
75	34	34	1222	275	3.44	1.79	NA	3	0	11	1	0	1.0
106	11	11	297	108	2.14	1.13	NA	9	158	237	164	19	0.73
108	19	14	509	891	1.24	0.61	92.1	1	1	0	0	0	0
111	22	23	1004	441	4.99	1.91	50.7	19	86	302	92	50	0.84
116	37	32	627	100	6.76	2.85	90.4	13	21	64	29	23	0.85
117	18	17	298	80	3.10	1.61	82.1	1	0	1	0	0	1.0
123	12	11	213		8.54	3.51	108.5	1	3	25	4	3	0.91

Fig. 1. Map of the Åland Islands showing the sampled patch networks (SINs) shaded in pink (high weevil occurrence) and blue (low weevil occurrence). Each gray dot represents a *Plantago lanceolata* patch. The number associated with each SIN is the ID number.
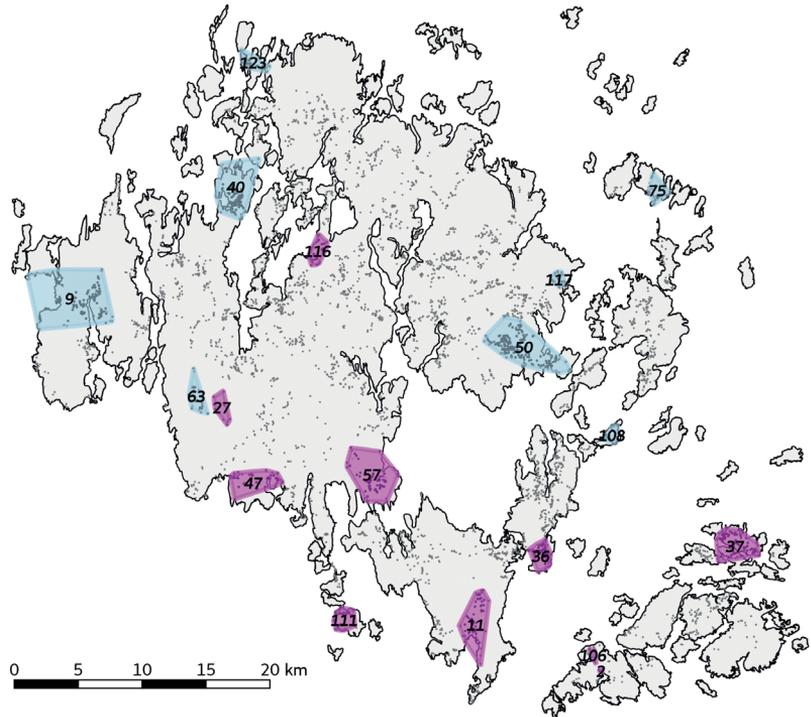
M. pascuorum, in which case most *E. vesicularis* individuals would be relatively large, or if it was both a primary parasitoid as well as a hyperparasitoid of *M. incultus*. If that were the case then there would be two size classes of *E. vesicularis*, one of which being smaller than *M. incultus*. We randomly selected one storage box of reared point-mounted individuals, and measured the length of each under a stereomicroscope with an ocular scale (0.05 mm accuracy). All individuals missing some body part(s) or glued in a curved position were excluded. The size measure was the body length from the front of the head to the end of abdomen (excl. ovipositor). A total of 346 female and 232 male *E. vesicularis*, and 66 female and 59 male *M. incultus* were measured.

Many parasitoids, including facultative hyperparasitoids can use host species of two sizes by using large hosts for female offspring and small hosts for male offspring (Macedo *et al.* 2014). To test whether *E. vesicularis* might be doing this we compared the SIN level sex ratio of *E. vesicularis* associated with rate of parasitism (*E. vesicularis*/all parasitized and unparasitized weevils) or potential hyperparasitism (*E. vesicularis*/[*M. incultus* + *E. vesicularis*]).

Statistical analyses

We used unweighted least-squares linear regression (Statistix 10.0, Analytical Software, Tallahassee, FL) to model associations of weevil abundance and parasitism rates of each wasp species with various variables. We modeled the mean abundance of weevils per spike (log-transformed) as a function of average connectivity of SINs, latitude, abundance of host plants (log-transformed), total parasitism rate (number of parasitoid individuals/[number of parasitoid individuals + number of weevil individuals]) and their first-order interactions. The mean per-spike weevil abundance was calculated for the occupied habitat patches within each SIN. The total number of spikes sampled from several patches was not recorded (missing values: SIN IDs 11, 27, 37, 40, 75 and 116 one patch; SINs 36 and 47 two patches; SIN 57 six patches). For these missing values we used the median of the recorded values from the SIN the patch was in. The total weevil abundance in a SIN was defined as the sum of both weevils and parasitoids that emerged in the rearing. Abundance of host plants was the sum of *P. lanceolata* coverage per SIN

in 2008. Host-plant coverage was not estimated for SINs 2, 75 and 106 in 2008. We estimated the host-plant coverage for these SINs by multiplying the mean coverage (5.745) of all patches in this study by the number of patches in the SIN. The spatial structure of the landscape can be quantified in several ways. We used average connectivity of patches within a SIN because it incorporates total area of habitat, patch size and distance between patches, which are all strongly correlated. The average connectivity was determined by first calculating the connectivity (*sensu* Moilanen & Nieminen 2002) of each patch based on its proximity to all other *P. lanceolata* patches, and the sizes of those patches, with mean dispersal distance of 0.25 km (dispersal kernel $\alpha = 0.025$), and then averaging the connectivities of the patches within each SIN (Table 1). We incorporated latitude to account for the apparent north–south gradient in weevil abundance (*see* Fig. 1).

We modeled rates of parasitism (the fraction of hosts parasitized) by the parasitoids *E. vesicularis* and *M. incultus* as a function of average connectivity, latitude, total host weevil abundance (log-transformed), parasitism rate by the other primary parasitoid species and their first-order interactions. For *M. incultus* we also used the parasitism rate by the hyperparasitoid *B. endemus*. We modeled the parasitism rate (the fraction of hosts parasitized) of the hyperparasitoid *B. endemus* as a function of average connectivity, latitude, total host abundance ($\log_{n+1}$-transformed), total abundance of *E. vesicularis* ($\log_{n+1}$-transformed) and their first-order interactions. In the analysis of *M. incultus* parasitism rate, there were several possible best statistical models because the variables latitude and weevil abundance were highly correlated. Therefore, as a *post-hoc* analysis, we used residuals of the linear regression of the parasitism rate of *M. incultus* as a function of latitude as the dependent variable in order to remove the strong effect of latitude. To compare the sizes of the parasitoids *M. incultus* and *E. vesicularis* we used an unpaired two-sample *t*-test. Finally, we tested the associations of SIN level sex ratio of *E. vesicularis* with the rate of parasitism and potential hyperparasitism with Spearman's rank-order correlation.

Results

The weevil *M. pascuorum* was present in 17 of the 18 patch networks sampled. However, its distribution at the landscape scale was strongly bimodal. In eight mostly northern SINs weevils were found in less than 9% of the patches, and in 10 SINs more than 39% of the patches were occupied (Table 1 and Fig. 2A–B). The reason for this spatially correlated bimodality (Fig. 1) is not explained by the effects of sampling effort, the total habitat area, average connectivity of patch networks, latitude or the abundance of the host plant (Figs. 2 and 3C).

Within occupied habitat patches within SINs, the mean number of weevils per spike was 0.80 (SD = 0.63), with at most 2.1 per spike. The density of weevils was unrelated to latitude, habitat patch connectivity in the patch network, and local density of *P. lanceolata*. However, there was a strong negative association between weevil density and the rate of parasitism (Fig. 3A and Table 2; $t = -4.89$, $p = 0.002$).

The primary parasitoid *M. incultus* was present in all but one of the patch networks occupied by the weevil, parasitizing 45%–100% of the weevils sampled (mean rate = 0.65, SD = 0.16). The rate of parasitism by *M. incultus* was low where the rate of parasitism by *E. vesicularis* was high (Fig. 3B and Table 2; $t = -3.14$, $p = 0.009$). Once the strong positive association with latitude was taken into account by using the residuals of the regression of *M. incultus* parasitism rate *vs.* latitude as the dependent variable, rate of parasitism was found to be related landscape connectivity and competition. Specifically, where patch connectivity was high (patches clustered together) the rate of parasitism by *M. incultus* tended to be low (Table 2; $t = -2.23$, $p = 0.047$).

The parasitoid *E. vesicularis* was present in all but two of the patch networks occupied by the weevil host, parasitizing 5% to 29% of the weevils sampled (mean rate = 0.18, SD = 0.09). The rate of parasitism by *E. vesicularis* was unrelated to habitat patch connectivity, latitude and host abundance (Fig. 3D). However, it decreased with the rate of parasitism by *M. incultus* (Fig. 3B and Table 2; $t = -5.63$, $p = 0.0001$). In order to determine the probable tro-

phic level of *E. vesicularis*, we compared its size with *M. incultus*. In both wasp species, females (*E. vesicularis*: mean length = 1.80 mm, SD = 0.27; *M. incultus*: mean length = 1.76 mm, SD = 0.25) were significantly longer than males (*E. vesicularis*: mean length = 1.32 mm, SD = 0.21; *M. incultus*: mean length = 1.21 mm, SD = 0.18) (*t*-test: *E. vesicularis*: t_{577} = 23.83, $p < 0.0001$; *M. incultus*: t_{124} = 13.83, $p < 0.0001$). There was no difference in length between the two species (*t*-test: females: t_{411} = 1.173, $p = 0.5$; males: t_{292} = 4.04, $p = 0.5$). The sex ratio of *E. vesicularis* among SINs was marginally female-biased (average female:male ratio: 0.54, SD = 0.14). No correlations were found between the SIN level sex ratio of *E. vesicularis* and the rate of parasitism (Spearman's correlation: r_S = –0.325, $n = 13$, $p = 0.280$) or the potential rate of hyperparasitism (r_S = –0.289, $n = 13$, $p = 0.334$).

The hyperparasitoid *B. endemus* was present in all but two of the habitat-patch networks occupied by its wasp host *M. incultus*. It parasitized the wasp in two to 26% of the weevils sampled (mean rate = 0.09, SD = 0.07). The rate of hyperparasitism was unrelated to any of the factors measured.

Discussion

The weevil

The biotic factors that influence population dynamics of a species can be resource limitation (bottom-up) and predators, parasites and diseases (top-down) interactions (Hunter & Price 1992). Classically, to observe top-down control we should detect delayed density dependence over time in the relationship between a predator and prey (Hunter *et al*. 1997) or conduct a predator exclusion experiment (Harrison & Cappuccino 1995, Kasparson 2016). At the scale of this study, there was no association of habitat connectivity or resource availability with density of *M. pascuorum*. Habitat patch connectivity may not be important because the patches are relatively stable, and large, and the weevil is very small (2–3 mm) so it may not be very mobile. Further, the vast majority of *P. lanceolata* seeds were left uneaten so we expected that the resi-

Table 2. Results of the unweighted least-squares linear regression analysis of weevil abundance and rates of parasitism.

Dependent variable	Predictor variable(s)	df	F	t	p
Log(mean weevil abundance per spike)	Total parasitism rate	1,14	23.95		0.0002
				–4.89	0.0002
E. vesicularis parasitism rate		1,13	31.71		0.0001
	M. incultus parasitism rate			–5.63	0.0001
Residuals of the regression *M. incultus* parasitism rate *vs.* latitude		1,14	21.07	4.59	0.0004
	E. vesicularis parasitism rate			–3.14	0.009
	Connectivity			–2.23	0.047
	Log(total weevil abundance)			0.61	0.553
	Connectivity × *E. vesicularis* parasitism rate			1.46	0.171
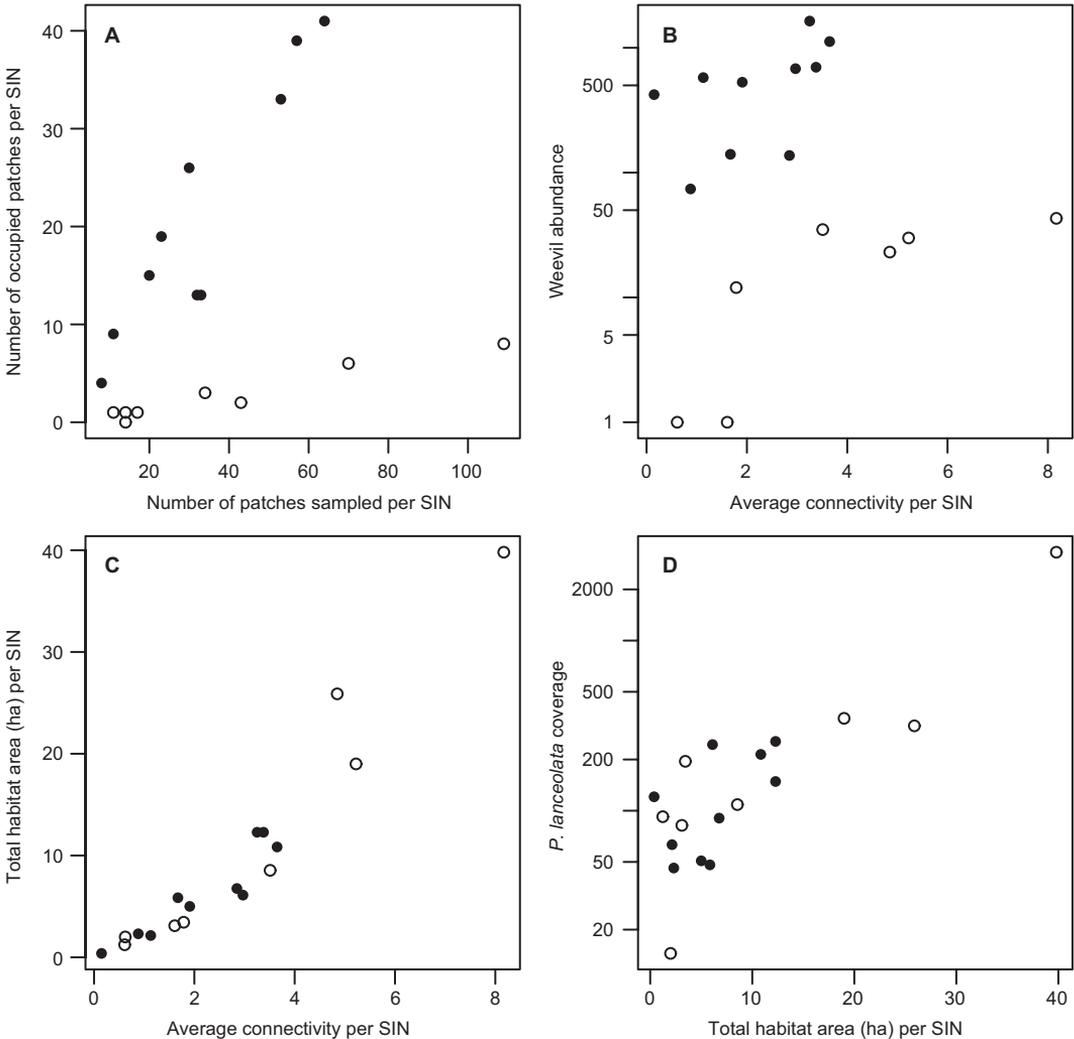
Fig. 2. Associations between (**A**) the number of patches in a semi-independent patch network (SIN) and the number of patches occupied by the weevil *Mecinus pascuorum*, (**B**) average patch connectivity in a SIN and abundance of *Mecinus pascuorum*, (**C**) average patch connectivity and the total habitat area of SINs, and (**D**) the total habitat area in a SIN and the total coverage of *Plantago lanceolata*. Each circle represents one SIN. Filled circles represent SINs with > 0.39 and circles SINs with < 0.09 occupancy rate.

dent populations of beetles were not on average resource limited. One explanation of why the weevil may not be resource limited is that it is on average parasitized at a very high rate. The data presented here are a snapshot in time, but by comparing semi-independent habitat-patch networks that differ in weevil host-density we see a negative association of host density with the rate of parasitism. Additionally, extremely high parasitism in the northern SINs (Fig. 1) due to the combined effects of the parasitoids *M. incultus*

and *E. vesicularis* (Table 1) apparently led to the association of weevil abundance with latitude (Fig. 3C), suggesting that on a large spatial scale the parasitoids may determine the distribution of the weevil. This local (SIN level) and regional (Åland Island level) associations with parasitism, along with the stability of the plant populations suggest that parasitoids play a considerable role in the dynamics of the weevil, which may be controlled from the top down.
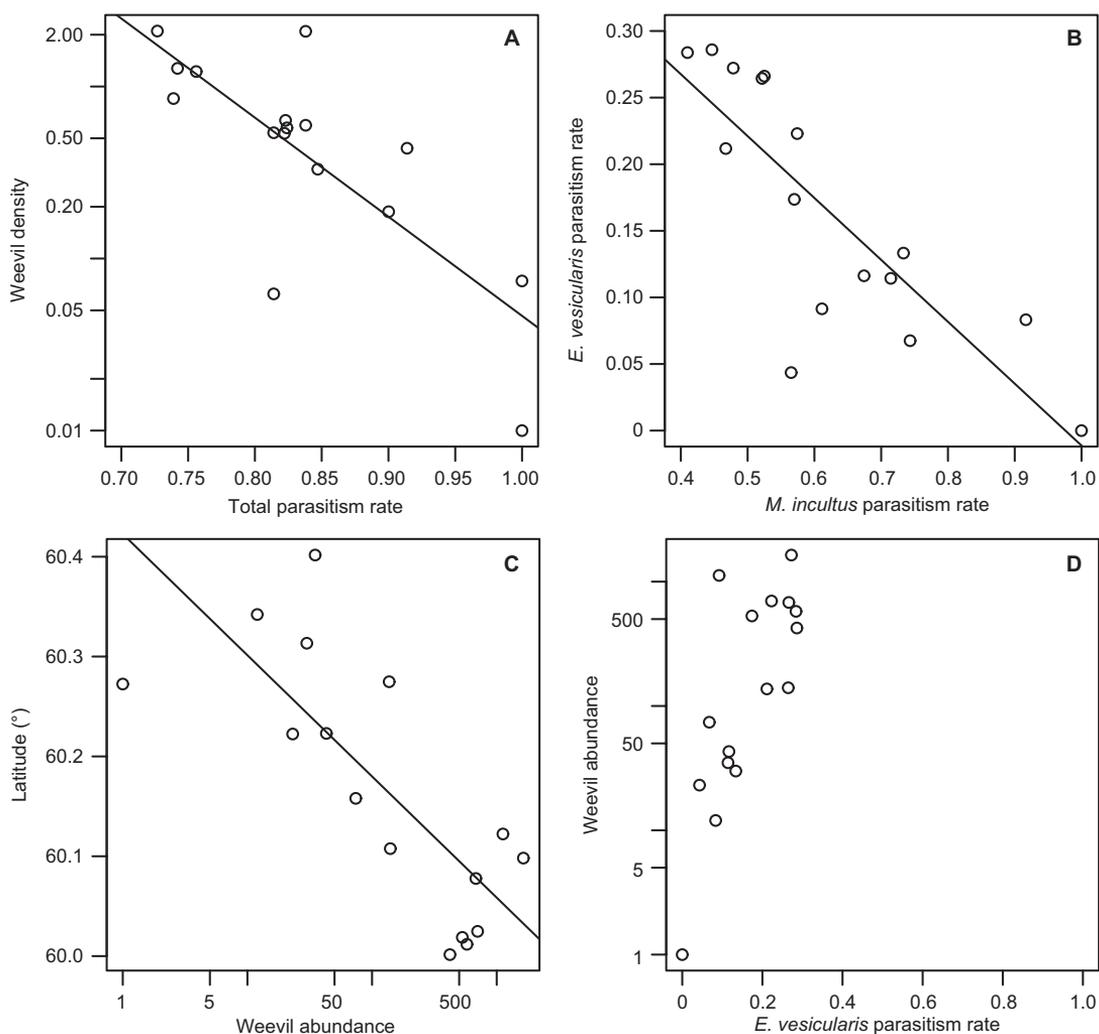
Fig. 3. Associations within each SIN (excluding SINs with no occurrence of the species) of (**A**) weevil density and the rate of parasitism, (**B**) rate of parasitism by *Eupelmus vesicularis* and *Mesopolobus incultus*, (**C**) latitude of the SIN midpoint and weevil abundance, and (**D**) weevil abundance and rate of parasitism by *Eupelmus vesicularis*.

The parasitoids *M. incultus* and *E. vesicularis*

On average 80% of the weevils were parasitized which is a very high rate of parasitism (Hawkins 1994). *Mesopolobus incultus* made up most of this, however, *E. vesicularis* was also abundant, and there was a strong negative association between the two parasitoids (Fig. 3B). This pattern could occur if there were direct competition between parasitoids, or if one parasitoid were a hyperparasitoid of the other. The natural history of the parasitoid *E. vesicularis* is not well

known, but it is a generalist, and has been considered both a parasitoid of *M. pascuorum* and a hyperparasitoid of *M. incultus* (Bouček 1977, Noyes 2013). An immature hyperparasitoid is restricted to feeding on a single host individual and cannot have perfect conversion efficiency so it will be significantly smaller than its host (Sullivan & Völkl 1999, Hatton *et al.* 2015). In our sample, *M. incultus* and *E. vesicularis* individuals were of the same length, though *E. vesicularis* was slightly slenderer. *Eupelmus vesicularis* individuals that developed as hyperparasitoids of *M. incultus* should be noticeably

smaller than *M. incultus* and much smaller than those developing in *M. pascuorum*. However, we found only one size class of *E. vesicularis*. Finally, if *E. vesicularis* used both hosts but lay male eggs in *M. incultus* we would expect a male bias where the ratio of *E. vesicularis* to *M. incultus* was high because male eggs would be laid in smaller hosts. We found instead that the sex ratio was equal in the different patch networks. Based on these three factors, the length of *E. vesicularis*, the single size class and the consistent sex ratio, we think it is most plausible that *E. vesicularis* acts merely as a primary parasitoid in this system. It follows from that, that the negative association of the two parasitoids is due to competition for hosts (Teder *et al.* 2012).

Competing parasitoids can coexist if they have different resource needs or strategies for host use. In a landscape context this might occur, for example, if a superior local competitor is an inferior disperser, allowing the other parasitoid to persist as a fugitive (Amarasekare 2003, Bonsall *et al.* 2004, van Nouhuys & Punju 2010); in our case, the specialist parasitoid *M. incultus* parasitizes at the highest rates at low patch-connectivity and high host-abundance (Table 2). Had *E. vesicularis* shown the opposite trend we might have concluded that *E. vesicularis* is the superior local competitor and inferior disperser. Indeed, it probably persists well locally because it does not depend on a single host species. It is also a poor disperser because females are brachypterous (Nieminen & Vikberg 2015). Furthermore, the negative association of the two parasitoids is strongest at high connectivity (Table 2), which suggests that dispersal limitation may constrain *E. vesicularis* to well-connected patches of suitable habitat. While the idea of co-existence due to a trade-off between local competitive ability and dispersal ability is a compelling scenario, and has rarely if ever been shown to occur in insect communities (Amarasekare 2003, 2007, van Nouhuys & Punju 2010), it is worthy of further study in this system.

Though hyperparasitoids are generally much smaller than their parasitoid hosts (Sullivan & Völkl 1999, Hatton *et al.* 2015), a hyperparasitoid will be nearly the size of its host if it develops extremely efficiently. Harvey *et al.* (2006) found such an exceptional case. They showed that when using pupae of the parasitoid *Cotesia glomerata*, the hyperparasitoid *Gelis agilis* develops to 90% its host mass, and *Lysibia nana* reaches 95% host mass. If this were the case in the weevil parasitoid community then the negative association between the two wasps can be partly due to strong variation of the rate of hyperparasitism (from 7 to 40% of *M. incultus*), which is strongest at high connectivity due to low mobility of *E. vesicularis*.

The hyperparasitoid *Baryscapus endemus*

The hyperparasitoid *B. endemus* is relatively common, parasitizing up to 26% of *M. incultus*. However, we found no association of the hyperparasitoid with factors that we measured. This suggests that the population size of *B. endemus* is independent of that of the host *M. incultus*, presumably because it has other hosts in the landscape, including several other parasitoids of the family Pteromalidae, even within the *P. lanceolata* weevil metacommunity (Nieminen & Vikberg 2015). Though we found no direct association between *B. endemus* and its host *M. incultus*, the hyperparasitoid can still influence the competitive relationship between the two primary parasitoids of the weevil by decreasing the population size of *M. incultus*.

Dynamics of the community

At the base of this community is an abundant host plant, *P. lanceolata*, associated with a few generalist and a few specialized herbivores, one of which is the specialist seed predator weevil *M. pascuorum* (Nieminen & Vikberg 2015). As in most insect communities (Hawkins 1994) there are many species of parasitoids associated with the weevil, however all but three are relatively rare (Nieminen & Vikberg 2015). The specialist parasitoid *M. incultus* parasitizes the largest fraction of hosts and is hyperparasitized by *B. endemus*. The generalist parasitoid *E. vesicularis* which could be both a primary or hyperparasitoid probably acts mostly as a primary parasitoid in this community.

Plantago lanceolata provides a stable resource for the weevil in the Åland Islands where it is common throughout much of the islands, independent to landscape structure (habitat connectivity and geographic position) and local *P. lanceolata* (host plant) density. While weevil density (number of weevils per seed spike) was independent of the environmental parameters, it was strongly negatively related to the rate of parasitism suggesting top-down control of the weevil by parasitoids. Without more data or experimentation, we cannot be sure that there is a strong trophic cascade in this system. However, if the suggestive pattern is robust, the next question is: why is it top-down rather than bottom-up? Strong top-down effects on communities are more commonly found in aquatic systems (e. g. Boaden & Kingsford 2015) than in terrestrial insect communities (Harrison & Cappuccino 1995), but this difference has been strongly debated (reviewed in Shurin *et al*. 2006). Differences in primary productivity (Strong 1992, Shurin *et al*. 2006), characteristics of the herbivores, higher trophic-level species and methods of study (Polis 1999, Borer *et al*. 2005) have all been used to explain the strength of trophic cascades.

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