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Strong dispersal in a parasitoid wasp overwhelms habitat fragmentation and host population dynamics

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Abstract

The population dynamics of a parasite depend on species traits, host dynamics and the environment. Those dynamics are reflected in the genetic structure of the population. Habitat fragmentation has a greater impact on parasites than on their hosts because resource distribution is increasingly fragmented for species at higher trophic levels. This could lead to either more or less genetic structure than the host, depending on the relative dispersal rates of species. We examined the spatial genetic structure of the parasitoid wasp *Hyposoter horticola*, and how it was influenced by dispersal, host population dynamics and habitat fragmentation. The host, the Glanville fritillary butterfly, lives as a metapopulation in a fragmented landscape in the Åland Islands, Finland. We collected wasps throughout the 50 by 70 km archipelago and determined the genetic diversity, spatial population structure and genetic differentiation using 14 neutral DNA microsatellite loci. We compared the genetic structure of the wasp with that of the host butterfly using published genetic data collected over the shared landscape. Using maternity assignment, we also identified full-siblings among the sampled parasitoids to estimate the dispersal range of individual females. We found that because the parasitoid is dispersive, it has low genetic structure, is not very sensitive to habitat fragmentation and has less spatial genetic structure than its butterfly host. The wasp is sensitive to regional rather than local host dynamics, and there is a geographic mosaic landscape for antagonistic co-evolution of host resistance and parasite virulence.

Keywords: DNA microsatellites, *Hyposoter horticola*, maternity analysis, *Melitaea cinxia*, metapopulation, spatial genetic structure

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Introduction

Parasites are limited to the locations in which their hosts occur. The population dynamics of parasites depend on their own traits, such as dispersal rate, as well as their host dynamics and the environment they inhabit. Like any other species, their dynamics are then reflected in the genetic structure of the population (Maze-Guilmo *et al.* 2016). Habitat fragmentation, or discontinuous resource distribution generally, is an important component of population dynamics (Hassell 2000) and can shape the genetic structure of a population through reduced gene flow and increased genetic drift (Whitlock 2004). In principle, higher trophic-level species should be more sensitive to habitat fragmentation than their prey or host species because their resources are increasingly unstable and sparsely distributed (Holt *et al.* 1999). Indeed, focusing on arthropods, habitat fragmentation has been shown to greatly influence the distribution, population dynamics and genetic structure of herbivores and their parasitoids, and to differ among species at different trophic levels (see reviews by Holt 2002; Cronin & Reeve 2005 and van Nouhuys 2016).

A review of movement and population dynamics of hosts and their parasitoids in heterogeneous landscapes

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by Cronin & Reeve (2005) showed that most parasitoids disperse less than their hosts (also see Roland 1993; Kruess & Tscharntke 1994; Komonen *et al.* 2000). The spatial genetic structure of a population is to a large extent influenced by population size and the movement of individuals in a landscape (Wright 1969). Thus, we expect greater genetic structure of these less-mobile parasitoids, in comparison with their hosts. Examples of this include the gall fly parasitoid *Eurytoma robusta* (Johannesen & Seitz 2003), *Neotypus melanocephalus*, a parasitoid of Lycinid butterflies (Anton *et al.* 2007), and the parasitoid wasp *Cotesia melitaearum* that parasitizes the Glanville fritillary butterfly, *Melitaea cinxia* (Kankare *et al.* 2005). Under these conditions, when the parasitoid population dynamics follow those of their hosts, there is the potential for the host–parasite interaction to persist regionally via metapopulation processes (local extinction–colonization dynamics) (Nee *et al.* 1997). If gene flow is sufficiently limited, we might also expect local antagonistic co-evolution of parasitoid virulence and host susceptibility, akin to some models of disease evolution (Keeling *et al.* 2004).

Alternatively, a parasitoid may move at a large spatial scale, avoiding the instability of local host dynamics, even those due to habitat fragmentation (Weisser 2000; van Nouhuys 2005; Cagnolo *et al.* 2009; Brückmann *et al.* 2011). Under this scenario, the genetic structure of the parasitoid should be lower than that of the host, as the breeding population of the parasitoid would span over multiple local host populations. Such is the case for *Lysiphlebus hirticornis*, a specialist parasitoid of the aphid *Tanacetum vulgare* (Nyabuga *et al.* 2012), and *Sycoscapter* sp, a parasitoid of the fig-pollinating wasp *Pleistodontes imperialis* (Sutton *et al.* 2016). Under this scenario, the persistence of the interaction cannot be due to metapopulation processes, but local dynamics of the host may be altered by the parasitoid. For instance, in an analogous host–pathogen system, colonies of the North American prairie dog (*Cynomys ludovicianus*) in Colorado have a metapopulation structure where the plague is present, but a continuous population where the plague is absent (George *et al.* 2013). The co-evolutionary interaction between closely interacting species can also be complex where the genetic structures of the antagonists or mutualists differ, resulting in a geographic mosaic where the strength of selection and the potential for evolution differ geographically for each species (Althoff & Thompson 1999; Thompson 2005).

We investigate the multitrophic system consisting of the parasitoid wasp *Hyposoter horticola* (Gravenhorst) (Ichneumonidae: Campopleginae) and its host, the Glanville fritillary butterfly *Melitaea cinxia* (Lepidoptera: Nymphalidae). The solitary endoparasitic egg-larval parasitoid (7 mm body length) has no other host species in Åland (van Nouhuys & Ehrnsten 2004; Shaw *et al.* 2009). The host has a metapopulation structure and is constrained by habitat fragmentation in the landscape (Hanski 2011). Studies based on distribution and behaviour have shown that the parasitoid is present in almost all local host populations and discovers new local host populations even within the same year the host colonizes a patch (van Nouhuys & Hanski 2002). Furthermore, in a previous genetic study, Kankare *et al.* (2005) detected low levels of genetic differentiation for the parasitoid population, but lacked a statistical power to draw decisive conclusions based on just four DNA microsatellite markers.

In this study, we assess the spatial genetic structure of the parasitoid *H. horticola* and compare it with its host, in a shared landscape. We also assess the role of habitat fragmentation in explaining the parasitoid genetic population structure by comparing the gene diversity of the wasp population in parts of the landscape that differ in the distribution of suitable habitat and host population size. Finally, we assess the dispersal range of individual females by identifying full-siblings among the sampled parasitoids in order to link genetic structure to individual dispersal. Based on theory and previous studies, we expect the parasitoid population to have low genetic structure, and not be strongly influenced by host dynamics or habitat structure.

Materials and methods

Study system

In the Åland Islands, a Finnish 50 × 70 km archipelago situated in the Baltic Sea between Sweden and mainland Finland, the butterfly lives as a classical metapopulation in stochastic balance between local extinctions and colonizations. In any given year, around 500 of the nearly 4000 potential habitat patches are occupied (Hanski 2011). The discrete patches of suitable habitat are typically small (<1 ha) dry meadows containing the butterfly's host plants, *Veronica spicata* and *Plantago lanceolata* (Plantaginaceae) (Kuussaari *et al.* 2004), and have been delimited using GPS coordinates (Ojanen *et al.* 2013). The meadows are naturally clustered in the landscape, forming semi-independent patch networks (SINs) (Fig. 1) separated from one another by at least 1.5 km of unsuitable habitat such as forest or water (Hanski *et al.* 1996; Ojanen *et al.* 2013). The SINs differ in size, patch number, patch connectivity and in their capacity to support the butterfly metapopulation (Hanski 2011).

The butterfly metapopulation is genetically structured at several hierarchical levels. At the smallest scale, both

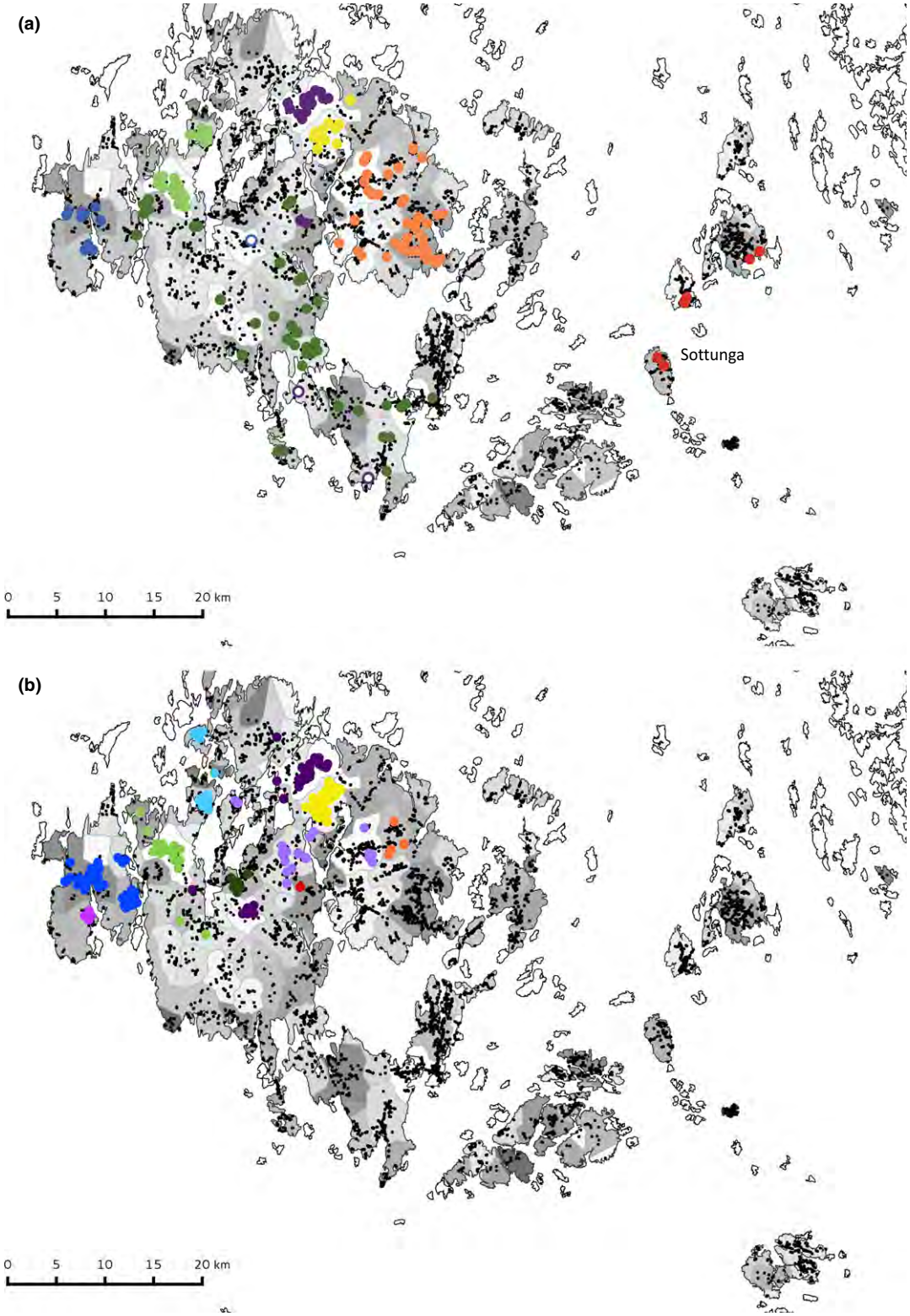

Fig. 1 Map of the *Hyposoter horticola* (a) and *Melitaea cinxia* (b) populations in the Åland Islands. The black dots represent the patches of suitable habitat for the host, and the different shades of grey represent the different semi-independent patch networks (SINs). Coloured full circles represent the sampled patches. Different colours indicate genetically significantly distinct clusters (seven for the parasitoid, 10 for the host), as detected by the spatial clustering of groups analysis in BAPS. The open circles in (a) represent the samples removed from the analysis.

larval nests (gregarious family groups) within local populations (habitat patches) and local populations themselves are significantly differentiated from each other (Orsini *et al.* 2008; Hanski 2011). At a larger scale, there is weak but significant isolation by distance (IBD) across the landscape (Saccheri *et al.* 2004). Corresponding to the genetic studies, extensive empirical (Hanski *et al.* 1994; Kuussaari *et al.* 1996; van Nouhuys & Hanski 2002; Ovaskainen *et al.* 2008) and modelling (Hanski *et al.* 2000; Ovaskainen 2004) research shows that 15–40% of individuals disperse to neighbouring patches, with those that leave the patch travelling on average only 300–400 m, resulting in genetic differentiation among habitat patches due to Allee (Kuussaari *et al.* 1998) and founder (Austin *et al.* 2011) effects. The parasitoid, which has no other host species in Åland, is present in almost all the local host populations, and in virtually all host nests, about a third of the caterpillars are parasitized (van Nouhuys & Ehrnsten 2004; Montovan *et al.* 2015).

Data collection

Melitaea cinxia caterpillars build conspicuous silken nests in which they gregariously feed, and spend the winter in diapause (Kuussaari *et al.* 2004). In the autumn 2009, three individuals from each nest were sampled from each local host population found in the Åland metapopulation (Ojanen *et al.* 2013). The fifth-instar caterpillars and the parasitoids growing inside them were maintained through winter diapause at 3 °C. In spring 2010, they were reared to adulthood under controlled laboratory conditions (12-h/12-h light/dark cycle, 28 °C/8 °C), feeding on *P. lanceolata* leaves. Upon eclosion, the adult parasitoids were put in 96% ethanol and stored at −20 °C until use.

Approximately a third of the caterpillars were parasitized by *H. horticola*, and about a quarter of those were hyperparasitized by *Mesochorus* cf. *stigmaticus* (Hymenoptera: Ichneumonidae) (Montovan *et al.* 2015). All of the female *H. horticola* parasitoids that survived to adulthood (about half of the hosts regularly die during diapause) were genotyped at 14 neutral DNA microsatellite loci specific to *H. horticola*: Hho3 (Kankare *et al.* 2004) and Hho11, Hho12, Hho13, Hho15, Hho16, Hho17, Hho18, Hho19, Hho21, Hho22, Hho23, Hho24 and Hho25 (Couchoux *et al.* 2015b). We focussed on females because male Hymenoptera are haploid, so they carry only half of the genetic information that diploid females do and can yield ambiguous results. Two females were excluded due to missing data for at least five loci. Thus, the final data set consisted of 407 females from 168 patches in 39 SINs (Fig. 1). All loci studied were in Hardy–Weinberg equilibrium (HWE) at the SIN level, but there was a heterozygote deficiency at the whole population level, and there was no linkage disequilibrium between any pairs of loci. Detailed methods and general characteristics of the DNA microsatellite loci used are given in Couchoux *et al.* (2015b).

Genetic data for the butterfly were obtained from Orsini *et al.* (2008). We used 10 neutral SNPs and four DNA microsatellite loci for 726 caterpillars of both sexes from 115 habitat patches in 20 SINs, collected in 2002 from the northern part of the study area. We reanalysed the data to match our analyses of the parasitoid in order to compare the spatial population structures of the two species.

Population genetics analysis

We explored the spatial genetic structure by performing a Bayesian clustering analysis (Corander *et al.* 2008; Cheng *et al.* 2013) using the spatial clustering of groups model in BAPS, which estimates the posterior probability for the optimal number of clusters (Corander *et al.* 2003). In our parasitoid sample of 407 individuals from 168 habitat patches, only a small number of samples came from each patch, so there were not enough data for a meaningful per-patch analysis. Therefore, we grouped individuals by SIN instead. The same analyses were performed on both the whole parasitoid data set and, in order to corroborate our result, using only the samples collected from the same SINs as the butterfly for a matched comparison (12 SINs, 220 and 646 parasitoid and butterfly individuals, respectively). The sampling scheme for the butterfly and the parasitoid was not identical. Almost twice as many butterflies as parasitoids were sampled, from roughly the same number of patches (parasitoid: 168; butterfly: 183), but from fewer SINs than the parasitoid (parasitoid: 39; butterfly: 25).

For both the butterfly and the parasitoid, we partitioned the genetic variation to different hierarchical levels and estimated *F* indices among sampling units at different hierarchical levels. We performed an AMOVA in Arlequin (Excoffier & Lischer 2010), where the hierarchical levels were based on the distribution of the habitat (Ojanen *et al.* 2013) and the genetic clustering above: (i) habitat patches, (ii) SINs and (iii) genetic clusters resulting from the spatial analysis in BAPS. We tested whether *F* indices were significantly larger than zero using permutation tests (1000 permutations). As AMOVA accommodates only two intermediate hierarchical levels, we tested two different models: habitat patches nested within SINs and SINs nested within genetic clusters. Host larvae in a nest are offspring of a single female butterfly (Hanski *et al.* 1994), and a host nest is usually

parasitized by a single female wasp (Couchoux *et al.* 2015a). Consequently, both the host larvae and most parasitoids emerging from one nest are full-siblings. To avoid the bias from including multiple closely related individuals in the data, we analysed only a single host individual and only a single parasitoid from each host nest. Furthermore, we excluded singleton populations from the analysis, that is patches or SINs represented by only one individual, to avoid the bias due to small sample size. Thus, depending on the model, the analysed data sets consisted of either 244 females in 73 patches or 333 females in 33 SINs for the parasitoid, and 660 individuals in 109 patches or 726 individuals in 20 SINs for the butterfly. Because the estimates of genetic differentiation among populations (F_{ST}) are affected by the level of genetic diversity (Hedrick 1999; Jakobsson *et al.* 2013), we analysed the butterfly data separately for SNPs and DNA microsatellites.

We assessed IBD for the parasitoid by calculating the correlation between pairwise genetic and geographic distances of habitat patches (Rousset 1997) using the parasitoid data set consisting of 244 females in 73 patches. Genetic differentiation was estimated as Wright's F_{ST}, using Weir & Cockerham (1984) estimator. We converted the pairwise F_{ST} estimates to $F_{ST}/(1 - F_{ST})$ for linearity and used a natural logarithm of the pairwise geographic distances. The calculation was made using Genepop (Raymond & Rousset 1995; Rousset 2008), and the significance was assessed using permutation tests (1000 permutations) (Mantel 1967).

For SINs with at least 10 parasitoids samples, we also calculated Nei's unbiased gene diversity (H_E) (Nei 1987) using EXCEL MICROSATELLITE TOOLKIT version 3.3.1 (Park 2001). Landscape parameters differ between SINs, which influences host population and evolutionary dynamics (Hanski 2011; Fountain *et al.* 2016). Thus, they could also influence population structure of the wasp. In each SIN, we measured (i) the size (the number of nests in a habitat patch) and age (the number of consecutive years the patch has been occupied, as a measure of the turnover of local host populations) of the local butterfly populations and (ii) habitat fragmentation as the number of patches per ha of suitable habitat in the SIN and the proportion of the landscape that is suitable in the SIN (areas were measured using spatial coordinates). We calculated the local population size as an average over 5 years using long-term survey data of the host butterfly (Ojanen *et al.* 2013) because the metapopulation structure of the host is unstable so its potential influence on wasp genetic structure will not be accurately represented by a single year (Orsini *et al.* 2008). We compared the H_E among SINs, and the host population size and age among SINs using Kruskal–Wallis rank sum tests in R (R Core Team 2012).

Dispersal analysis

We estimated the dispersal range of successfully reproducing parasitoid females using maternity assignment of siblings in the data set, based on the DNA microsatellite genotypes. The 407 female offspring sampled were assigned to full-sibling groups using the full-likelihood method implemented in COLONY 2.0.3.1 (Wang 2004). We performed one medium run with a 10^{-4} genotyping error rate, and assumed monogamy as the reproductive system. As a test, we ran the analysis on parasitoid offspring coming from the same host cluster in 10 host clusters allowing polyandry, but the proportion of polyandrous females and the level of polyandry became unrealistically high, particularly as we expect polyandry in our system to be rare or even nonexistent (Ridley 1993).

Then, we mapped the geographic distances between siblings to assess the minimum dispersal range of their mother. For each full-sibling group, we used the longest distance between siblings as an estimate of the minimum dispersal range of the mother. Geographic coordinates were available for each habitat patch (Ojanen *et al.* 2013), but not for each individual host nest, so mothers whose offspring were all located within the same patch were assigned a dispersal distance of zero.

Results

Population genetics

Bayesian clustering of SINs showed that both the parasitoid and the butterfly populations in the Åland Islands are genetically structured. For the parasitoid, there were seven genetically differentiated clusters of SINs with a high probability ($k = 7$, $P = 1$), and for the butterfly, there were 10 ($k = 10$, $P = 1$). These genetic clusters were spatially segregated (Fig. 1). Three SINs were each represented by only a few parasitoid individuals coming from the same patch or the same nest, which may not accurately represent the allele frequencies in their SIN. Consequently, samples from these patches (open circles on Fig. 1a) were not spatially connected to the main distribution of the patches in their genetic cluster. We considered them to be statistical anomalies and reran the analysis without these three SINs, which did not change the results. When the analyses were conducted using butterfly and parasitoid samples from matched SINs (only the 12 northern SINs), the parasitoid population was structured in five clusters ($k = 5$, $P = 0.88$) and the host in nine ($k = 9$, $P = 1$).

All hierarchical levels harboured a significant amount of genetic variation for both species. The only exception

was the individual level in the parasitoid, where the inbreeding coefficient (F_{IP} and F_{IN}, Table 1) was not significantly larger than zero. In the butterfly, the most prominent difference in the results between SNP and DNA microsatellite markers was the higher inbreeding coefficients (F_{IP}, F_{IN} and F_{IT}, Table 1) in the latter. However, all estimated inbreeding coefficients were significantly larger than zero. Genetic differentiation among genetic clusters and inbreeding within them was also significantly greater than zero for both the parasitoid and the host (parasitoid: $F_{CT} = 0.04$, $P < 0.001$; $F_{IT} = 0.12$, $P < 0.001$; host: SNPs: $F_{CT} = 0.01$, $P < 0.01$, $F_{IT} = 0.29$, $P < 0.001$; DNA microsatellites: $F_{CT} = 0.03$, $P < 0.001$, $F_{IT} = 0.44$, $P < 0.001$).

Genetic and geographic distances between pairs of patches were significantly correlated in the parasitoid population ($r = 0.04$, $P < 0.001$), showing IBD (Fig. 2). The average gene diversity of the parasitoid across loci (H_E) at the level of SINs ranged from 0.41 to 0.52, but did not vary significantly among SINs (Kruskal–Wallis rank sum test: $\chi^2 = 3.20$, d.f. = 10, $P = 0.98$). This was true even though the SINs differed in local host population sizes (Kruskal–Wallis rank sum test: $\chi^2 = 53.33$, d.f. = 10, $P < 0.001$) and ages (Kruskal–Wallis rank sum test: $\chi^2 = 61.27$, d.f. = 10, $P < 0.001$), degree of fragmentation of suitable habitat [from 3.57 to 6.66 patches/ha of suitable habitat (mean = 4.62, SD = 0.96)] and the fraction of habitat in the SIN that is suitable [from 0.6% to 2.0% of area (mean = 1.07, SD = 0.43)] (Fig. 3).

Parasitoid dispersal

The 407 female parasitoid offspring analysed were mothered by 216 different females. Ninety-three (23%) of the analysed females did not have siblings in the sample and the rest were clustered into 123 sib groups. Sib groups consisted of two to 11 offspring (mean = 2.6; median = 2) distributed in one to six host nests (mean = 2; median = 2), one to four habitat patches (mean = 1.6; median = 2) and one or two SINs. Of the 123 sib groups, only 25 (20%) were restricted to a single host nest and the rest were spread to more than one nest, either within a single habitat patch (37%) or in several patches (42%). Sixteen of the latter had offspring in two different SINs.

Most of the mothers with offspring in multiple host nests dispersed <1000 m. Approximately half (46 of 98) had offspring sampled from only one patch, and therefore, their dispersal range was recorded as zero. But those with offspring sampled from multiple patches (52 of 98) travelled 2082 m on average and up to 7462 m (Fig. 4).

Table 1 Analysis of molecular variance (AMOVA)

	DNA microsatellites			SNPs		
Source of variation	Variation (%)	*F*	*P*	Variation (%)	*F*	*P*
a. Parasitoid						
Model = Patches nested within networks						
Among networks	7.32	$F_{NT} = 0.07$	**<0.001**			
Among patches within networks	8.52	$F_{PN} = 0.09$	**<0.001**			
Among individuals within patches	−5.31	$F_{IP} = -0.06$	0.99			
Within individuals	89.50	$F_{IT} = 0.11$	**<0.001**			
Model = Networks nested within genetic clusters						
Among genetic clusters	4.06	$F_{CT} = 0.04$	**<0.001**			
Among networks within genetic clusters	5.53	$F_{NC} = 0.06$	**<0.001**			
Among individuals within networks	2.24	$F_{IN} = 0.02$	0.1			
Within individuals	88.20	$F_{IT} = 0.12$	**<0.001**			
b. Host butterfly						
Model = Patches nested within networks						
Among networks	4.85	$F_{NT} = 0.05$	**<0.001**	6.78	$F_{NT} = 0.07$	**<0.001**
Among patches within networks	2.45	$F_{PN} = 0.03$	**<0.001**	6.91	$F_{PN} = 0.07$	**<0.001**
Among individuals within patches	36.80	$F_{IP} = 0.40$	**<0.001**	15.20	$F_{IP} = 0.14$	**<0.001**
Within individuals	55.90	$F_{IT} = 0.44$	**<0.001**	71.10	$F_{IT} = 0.18$	**<0.001**
Model = Networks nested within genetic clusters						
Among genetic clusters	2.92	$F_{CT} = 0.03$	**<0.001**	0.80	$F_{CT} = 0.01$	**<0.01**
Among networks within genetic clusters	2.36	$F_{NC} = 0.01$	**<0.001**	6.94	$F_{NC} = 0.07$	**<0.001**
Among individuals within networks	39.00	$F_{IN} = 0.41$	**<0.001**	21.39	$F_{IN} = 0.23$	**<0.001**
Within individuals	55.70	$F_{IT} = 0.44$	**<0.001**	70.87	$F_{IT} = 0.29$	**<0.001**

Abbreviations for *F* indices: I, individual; P, patch; N, network (SIN); C, genetic cluster; T, total.
Proportions of variation and *F* indices significantly larger than zero are indicated in boldface.

Discussion

Spatial structure of the parasitoid population

The parasitoid population was structured into seven genetic clusters identified by BAPS that were spatially mostly contiguous and clearly defined in terms of the isolation of the SINs, and were consistent with the previous information on the parasitoid dispersal, based on the records from patch occupancy and colonization of new local host populations (van Nouhuys & Hanski 2002). In a previous study, Kankare *et al.* (2005) found only three spatially mixed genetic clusters of the parasitoid in the Åland Islands. Our results showed, however, that the parasitoid population is spatially more structured and that the genetic clusters have clear geographic bounds. The discrepancy probably results from low sample size and a small number of DNA microsatellite markers used in the previous study (Kankare *et al.* 2005), preventing the detection of fine-scale genetic structuring.

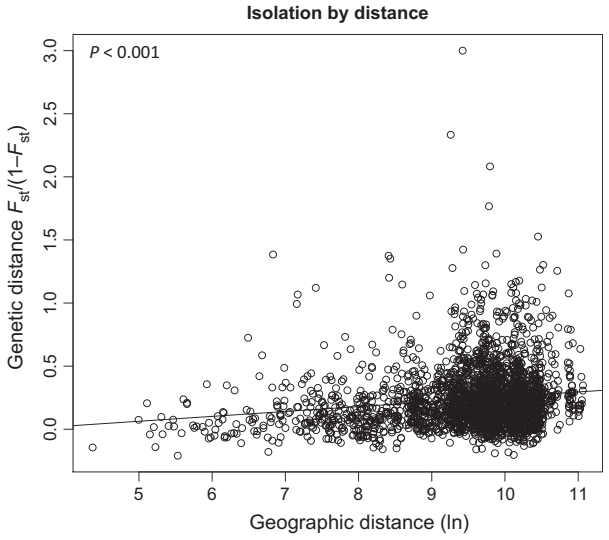

Fig. 2 Isolation by distance in the *Hyposoter horticola* population in the Åland Islands, as a correlation between pairwise genetic ($F_{ST}/(1 - F_{ST})$) and (ln) geographic distances between habitat patches.

There was, however, some geographic incongruence (dark green and purple clusters on Fig. 1a), which could be due to the fact that the number of individuals sampled per patch and SIN was sometimes low, especially in low host-density areas. We also found geographic structure where we did not expect it. As part of an experiment in 1991, host caterpillars that were naturally parasitized were introduced from Finström (purple in Fig. 1a) to Sottunga (identified in Fig. 1a), which had previously been unoccupied (Fountain *et al.* 2016). The population has persisted, but the Sottunga parasitoid samples from 2009 fall in the local eastern genetic cluster (red in Fig. 1) rather than the one used to colonize the island 18 years earlier, indicating that there has been strong introgression from nearby sources.

The AMOVA showed that the parasitoid population was hierarchically structured at the three levels tested: (i) local host populations, (ii) SINs (low levels

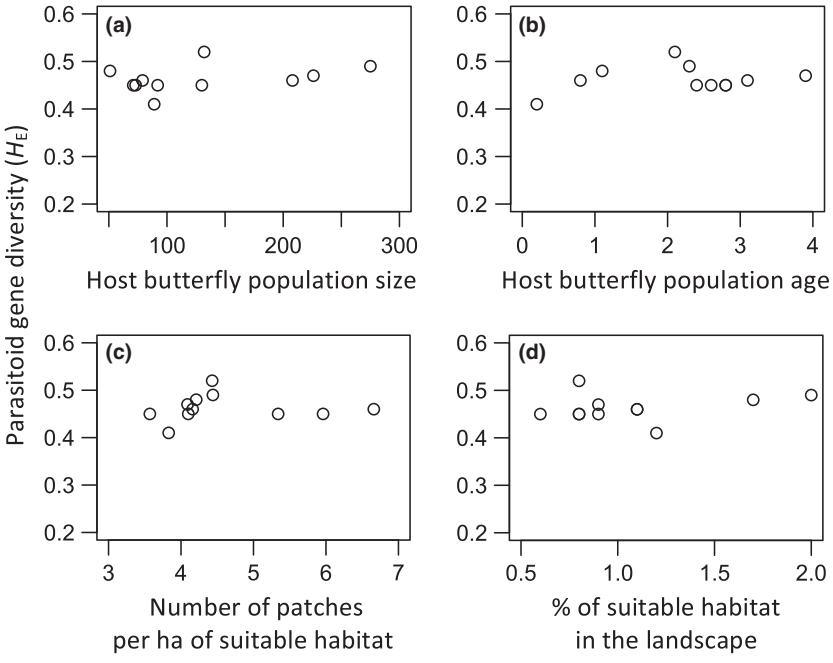

Fig. 3 The association of *Hyposoter horticola* gene diversity (H_E) at semi-independent patch network (SIN) level with aspects of host population dynamics: size (average total number of nests over 5 years) of the host *Melitaea cinxia* population in the SIN (a) and average age in years of the local host populations in the SIN (b); and habitat fragmentation: the number of patches per ha of suitable habitat in the SIN (c) and the proportion (in %) of landscape that is suitable habitat in the SIN (d).

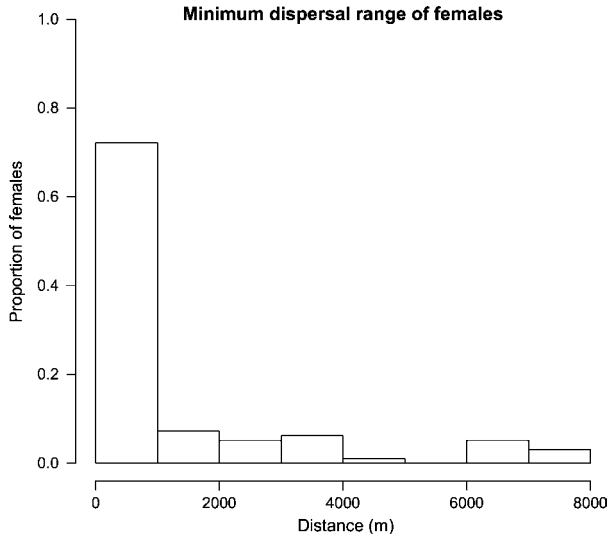

Fig. 4 Distribution of minimum dispersal range of *Hyposoter horticola* females, estimated as the longest geographic distance between full-siblings (data for 98 females, ranging from 0 to 7462 m).

determined by both the landscape and the distribution of the host butterfly) and (iii) Bayesian genetic clusters. The inbreeding coefficient was significantly larger than zero within genetic clusters, but not when the habitat patches or SINs were the lowest hierarchical level in the AMOVA. Indeed, inbreeding coefficient was negative when habitat patch was the lowest hierarchical level (F_{IP}), indicating a very small number of breeding females in each habitat patch and/or that males and females breeding in the same patch come from two genetically differentiated sources. On the other hand, inbreeding coefficient close to zero (F_{IN} = 0.02) and the estimated dispersal distance suggest that the level of SINs represents best the breeding population for the parasitoid. This is also supported by a positive inbreeding coefficient found at the level of genetic clusters (F_{IT} = 0.12), which most probably results from further substructuring in the data (Wahlund effect). The importance of habitat patches in spatial structuring is probably overestimated, as the comparisons among habitat patches are strongly affected by the founder effect and very small effective population size in the habitat patches. We also found a weak but significant pattern of IBD, indicating that in the Åland Islands the parasitoid population as a whole is not panmictic, with gene flow occurring commonly among patches, but being limited over longer distances.

Comparison of the parasitoid and the host

Bayesian clustering analyses similar to those performed on the parasitoid showed a strong spatial structure in the butterfly, which matches what was earlier found by Orsini *et al.* (2008). Local populations in the northern part of Åland were grouped into 10 genetic clusters, all of which were contiguous except one (purple on Fig. 1b). Genetic clusters correspond to the spatial scale of SINs in the butterfly, whereas they spanned further in the parasitoid. In the data for the 12 northern SINs with samples from both species, the butterfly and parasitoid were grouped into nine and five clusters, respectively, further supporting our hypothesis that the parasitoid population is genetically less structured than the host.

The AMOVA results for SNPs and microsatellites were quantitatively but not qualitatively different and showed that the butterfly population, like the parasitoid population, was hierarchically structured at three levels, at the level of Bayesian genetic clusters, SINs and habitat patches. Genetic clusters were larger for the parasitoid compared to the host and the inbreeding patterns also differed in between them (Table 1). Fast local population extinction–recolonization dynamics characterizes the host butterfly metapopulation, and as a result, their local populations experience recurrent founder effect and their effective population sizes are very small (Hanski 2011). Inbreeding coefficients were significantly larger than zero at all hierarchical levels. Previous observations have also shown that the butterflies mostly mate within their natal patch (Hanski *et al.* 1994; Kuussaari *et al.* 1996) and local populations apparently suffer from inbreeding depression (Saccheri *et al.* 1998; Haikola *et al.* 2001). Thus, the butterfly host appears to breed at a smaller scale than the parasitoid, perhaps only within the habitat patches. Determining the hierarchical level that precisely defines the breeding population in the host is difficult; however, as the local populations often consist of very few breeding individuals, the importance of the habitat patch level is boosted.

Gene diversity and ecological parameters

Population genetics theory predicts that habitat fragmentation reduces effective population size and gene flow via genetic drift and founder effect, leading to a decreased genetic diversity (e.g. Whitlock & Barton 1997; but see Corbett-Detig *et al.* 2015). The combined effects of habitat fragmentation and strong local host dynamics should amplify this effect for a specialist parasitoid wasp. In the Åland Islands, SINs vary in degree of habitat fragmentation (size, connectivity, the number of patches) and host population dynamics. However, we detected no association of genetic diversity in neutral genetic markers in the parasitoid with host population size or age, and increased fragmentation (as the proportion of suitable habitat in the landscape, or the

number of patches per ha of suitable habitat) was not associated with a decreased genetic variation. This suggests that the wasp is not constrained by habitat fragmentation or local host dynamics, which can be explained by the fact that genetic diversity in a structured landscape reflects the balance between drift and dispersal (Whitlock 2004; Hedrick 2011).

Dispersal

Genetic structure is influenced by size, age, history and origin of populations, as well as by the dispersal rate of a species (Bohonak 1999). If we find that the movement of individuals is consistent with genetic structure, then dispersal is likely to be an important part of the observed genetic structure (Slatkin 1987). Parasitoid dispersal varies greatly among species: from the order of metres in *Cotesia urabae* (Avila *et al.* 2013) or *Aphytis melinus* (Zappalà *et al.* 2012), to hundreds of metres in *Trichogramma* spp. (Kuske *et al.* 2003), to kilometres in *Nasonia vitripennis* (Grillenberger *et al.* 2009) and, when assisted by wind, even to tens of kilometres (Zavodna *et al.* 2005; Ahmed *et al.* 2009). This wide range of dispersal distances can explain why there is no clear pattern of response to habitat fragmentation in parasitoids, and why parasitoid species within the same multitrophic system can be affected differently by host dynamics and habitat fragmentation (Kankare *et al.* 2005; van Nouhuys 2005).

Sibship reconstruction based on molecular markers has been used a few times to estimate dispersal and foraging distances in insects (e.g. Charman *et al.* 2010; Lepais *et al.* 2010). By identifying full-siblings among parasitoid offspring and estimating the dispersal range of their mothers, we found that while the majority of parasitoid females moved little (<1 km), half of them moved among patches (local butterfly populations) and even up to 7.5 km. This is consistent with our results on genetic clustering as well as with a previous study using survey data that showed that the parasitoid was able to parasitize new host populations up to 6.8 km from established host populations (van Nouhuys & Hanski 2002). Empirical studies have shown that the butterfly disperses an average of 300–400 m and up to 3 km (Hanski *et al.* 1994; Kuussaari *et al.* 1996). Thus, like in the host–parasitoid system studied by Sutton *et al.* (2016), the parasitoid is more mobile than its host, dispersing at least twice as far. This and the AMOVA results show that the wasp both mates and produces progeny at a scale larger than does the butterfly.

Conclusion

The strong dispersal of the parasitoid leaves it little affected by habitat fragmentation or the metapopulation dynamics of its host. This is reflected in its spatial genetic structure and in its distribution in the landscape. The parasitoid occupies all local host populations, parasitizing one-third of the hosts in all host clusters, whatever their spatial isolation is, including newly colonized host populations. The host butterfly cannot avoid the detection at the local scale (within a habitat patch) (van Nouhuys & Ehrnsten 2004; van Nouhuys & Punju 2010) and also cannot escape parasitism by colonizing nearby unoccupied habitat patches.

Classically, metapopulation structure should allow antagonists such as hosts and parasites or competitors to persist regionally through the limited dispersal and local extinction–colonization dynamics (Nee *et al.* 1997). In our study system, the host butterfly lives as a metapopulation, but the parasitoid does not. The interaction persists in a way that is analogous to host-virulent disease (Hess 1996) rather than predator–prey (Hassell *et al.* 1994) dynamics, with some hosts being left unparasitized in each local population (Montovan *et al.* 2015) as analogous to a resistant fraction of the population. The parasitoid reduces local host population sizes, which increases the rate of local host extinction, but not its own.

The genetic structure of a population not only reflects its population dynamic, but also influences its potential for evolution (Ezard *et al.* 2009). Furthermore, it influences the potential for co-evolution of closely interacting antagonists, such as hosts and their parasites (e.g. Thrall *et al.* 2012). We found that the host and the parasitoid have mismatching population genetic structures. This creates a geographic mosaic landscape for traits under selection, such as those related to parasitoid virulence and host resistance (Thompson 2005). In this situation, selection on the host might be regionally constant because the parasitoid is present throughout the landscape. Response to selection by the host, however, might be limited by high local population turnover and low effective population size, potentially giving the parasite, which also has a relatively large breeding population, an evolutionary advantage.

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Data accessibility

Hyposoter horticola DNA microsatellite genotype data and habitat patches geographic coordinates are archived in Dryad. doi: 10.5061/dryad.s5k6k.