

Spatial pattern in checkerspot butterfly–host plant association at local, metapopulation and regional scales

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Received 25 Feb. 2005, revised version received 26 Apr. 2005, accepted 2 May 2005

Singer, M. C. & Wee, B. 2005: Spatial pattern in checkerspot butterfly–host plant association at local, metapopulation and regional scales. — *Ann. Zool. Fennici* 42: 347–361.

Host search behaviour and population dynamics of butterflies interact with host quality and dispersion to generate spatial distributions of insects at local, metapopulation and regional scales. At a local scale, search behaviour causes isolated plants to be more attacked than well-connected individuals. As scale increases this pattern is reversed and hosts in isolated habitat patches are less attacked than those in well-connected patches. In *Melitaea cinxia*, spatially variable host preferences generated biased colonization of habitat patches containing different hosts. In *Euphydryas editha*, a metapopulation in anthropogenic evolutionary disequilibrium used a novel host in disturbed patches and the traditional host in intervening habitat. The novel host was less preferred but supported higher fitness. When habitat patches were small, insects achieved higher densities in patches of the preferred host because of biased migration into those patches. When patches were large, density was higher on the less-preferred host because of high survival. Because biased movement of insects among hosts affects gene flow, it should also affect genetic differentiation among insects using different hosts. We investigate this question by describing host-associated genetic differentiation at local and regional scales.

Introduction

Distributions of herbivorous insects across landscapes can be generated both by predator–prey interactions and by plant–herbivore interactions. Harrison *et al.* (2005) describe a system in which predator–prey relations produce the principal spatial patterns and the plant serves as a passive but defoliable template against which the herbivore–enemy interactions are played out. In sharp contrast, in the checkerspot butterflies that are our subjects here, spatial complexities arise principally from plant–insect interactions. Below, we describe how this occurs. We switch

opportunistically among three very similar insect species, *Melitaea cinxia*, *Euphydryas editha* and *E. aurinia*, in order to describe the mechanisms that generate distributions of insects among hosts at three scales: the local scale within a habitat patch, the metapopulation scale among interacting populations and the regional scale among metapopulations. It is intuitive that these mechanisms should be scale-dependent (Doak 2000, Menendez & Thomas 2000). For example, we might expect the local distribution of insects to be governed mostly by their host preferences while their distribution among distant populations containing different hosts should be more

influenced by population dynamics on those hosts. Below, we provide evidence that this is indeed the case. As well as describing ecological and behavioural mechanisms that generate spatial patterns of plant–insect association, we summarize recent information about genetic correlates of host-association at local and regional scale. In themselves, these genetic patterns do not determine spatial patterns of insect-host association, but they provide clues about both past and present mechanisms that do so.

Insect host-relationships that generate spatial pattern

Variation in plant quality is a major cause of nonrandom patterns of insect–host association (Strauss & Karban 1998, Singer *et al.* 2002). Some of this plant variation is genetic, some is caused by conditions of the soil, light and moisture, and some comprises plant defenses induced by insect oviposition or feeding (Karbon & Baldwin 1997). Plants respond to the presence of insect eggs even prior to larval eclosion (Meiners & Hilker 2000) and these induced responses may deter subsequent oviposition, resulting in a regular dispersion pattern of eggs across the plant population. Potential immigrants to a patch may avoid it if it contains plants damaged by conspecifics (Herzig & Root 1996). A large literature documents how induced plant responses attract specific predators of herbivores (Dicke 1994) and parasitoids (Thaler 1999), which will generate indirect effects on herbivore spatial patterns. Direct conspecific attraction or repulsion (Nufio & Papaj 2001) mimic induced plant responses in their effects on herbivore dispersion. An occupied plant or habitat patch may be avoided either because ovipositing insects avoid conspecifics and/or because the plant has responded with induced resistance to the insects already present.

We have briefly described how spatial variation of plant quality is important to the plant–insect interaction. However, the quality of a plant is irrelevant to the insect if the plant is not encountered, and encounter depends on interactions between insect movement, insect population dynamics and plant dispersion. How does the risk of attack on a plant depend on its spatial

position with respect to conspecifics? Gripenberg and Roslin (2005) show that well-connected oak trees were more likely to bear populations of leaf miners than isolated oaks. The individual oaks acted as habitat patches in the landscape. However, among hosts of butterflies the reverse is often described: the risk to isolated plants may be greater than that to members of clumps (Mackay & Singer 1982, Root & Kareiva 1984). How does increased risk of isolated plants arise? Random search initiation by adults is the likely cause (Mackay & Singer 1982). If a butterfly starts to search in an area of high host density, each plant has a low risk of attack; if search begins in an area of low host density, each plant has a high risk. But where do butterflies start to search? If we were to examine a landscape from a height of, say, a kilometer, we would expect to see higher butterfly densities where host density is high because that is where the larvae feed and adults emerge. Viewed at this scale, searches would tend to be initiated in areas of high host density. However, as we approach closer and examine the system at finer scales, the points of search initiation become dissociated from local host density. This is because female butterflies spend most of their flight time searching for nectar or for places to bask and digest. During these activities they don't respond to hosts, so the point in space at which a female starts to search for a host becomes unrelated to local host density and isolated plants will be disproportionately attacked. How strong will this effect be? The manner in which randomly-moving insects partition their eggs depends on the reaction distance, the distance from which insects perceive and turn towards the plants. We can imagine each plant surrounded by a bubble and vulnerable to insects that by chance enter the bubble. If the reaction distance is small, a group of plants will be surrounded by a larger bubble than an isolated plant because the group is itself larger than the isolated plant. As reaction distance increases, the bubbles around isolated plants and around clumps converge in size and the risks to a group and to an individual converge on each other. Mackay and Singer (1982) studied captive populations of a butterfly, *Cissia libye* that had been observed to attack principally isolated plants in the field. Female *C. libye* lay single

eggs and fly after each oviposition, often basking for a while before starting the next oviposition search. Therefore, it did not seem unreasonable to assume that the position in the greenhouse where a search began was independent of the location of the previous oviposition, especially because these insects made no response to previously-laid eggs. If the risk to an individual was not affected by isolation, then the risk to a group of 20 plants should have been 20 times the risk to an isolated plant. In fact, the risk to a group of 20 was about three times the risk to an isolated plant, so the risk to an individual was much higher if it was isolated.

What's the reason for the opposite effects of host isolation observed in butterflies and in oak leaf miners (Gripenberg & Roslin 2005)? The likely reason is scaling of the habitat relative to the movement of the insects. The leaf miners presumably build up populations on individual trees on which many individuals spend their entire lives. Miners that do migrate probably do not sample very many trees before settling down again. As Gripenberg and Roslin remark, for their leaf-miners the single oak tree is a habitat patch.

Below, we switch to thinking about spatial patterns of host association that have been observed in checkerspot, using work on other species to help understand these patterns. Checkerspot spatial dynamics have been well-studied, especially in *Melitaea cinxia*, for which the distributions and abundances of both resources and natural enemies have been included in the project (Hanski & Meyke 2005). We describe pattern in our study insects at increasing scales, since the patterns at the regional scale are superposed on those at the metapopulation scale, which are in turn superposed on those at the local scale.

Checkerspot–host associations at the local scale

Consequences of foraging behavior

Studies of host search behavior have been concentrated on *Euphydryas editha*, especially the population at Rabbit Meadow, a montane site at 2350 m elevation in Tulare County, California. At this site the insects used two hosts, a rosette-

shaped perennial, *Pedicularis semibarbata* and an erect annual, *Collinsia torreyi*. Females searched visually, making innate responses to plant shape and leaf shape that were not modified by experience (Parmesan 1991, Parmesan *et al.* 1995) and typically encountering > 10 host plants prior to laying a single egg cluster (Mackay 1985). Because the reaction distance was large, we expected that isolated hosts should have the highest risk of attack, and indeed they did (Rausher *et al.* 1981). If adults don't trouble to travel far after feeding before searching for oviposition sites, their choice of host for oviposition can be influenced by the distribution of nectar sources. Murphy *et al.* (1984) showed that egg densities in a population of *Euphydryas chalcedona* declined with increasing distance from a concentration of nectar used by the adults.

Host search by larvae can cause the attack rate on one host species to be influenced by the proximity of another. At Rabbit Meadow, a habitat patch was studied in which oviposition by *E. editha* was exclusively on *Pedicularis*. Most larvae entering diapause in midsummer did so around the base of the individual plant on which they had been feeding. Diapause was broken in spring at snowmelt, often before the new *Pedicularis* shoots had emerged. Larvae wandering away from the *Pedicularis* ate and killed newly-germinated seedlings of *Collinsia torreyi*. Thomas (1986) found that when *E. editha* larvae were left undisturbed, the survival of *Collinsia* seedlings increased with increasing distance from the nearest *Pedicularis*. However, this effect disappeared in plots from which *E. editha* larvae were removed. Only when larvae were present did proximity of a *Pedicularis* increase the risk of *Collinsia* mortality. The insects mediated apparent competition (Holt 1977, Morris *et al.* 2005) between the plant populations, in the sense that the negative impact of *Pedicularis* on *Collinsia* mimicked the effects of competition between the two plants.

Genetic correlates of within-site diet variation in host association

When an insect population uses two or more host species (or host phenotypes), the possibility

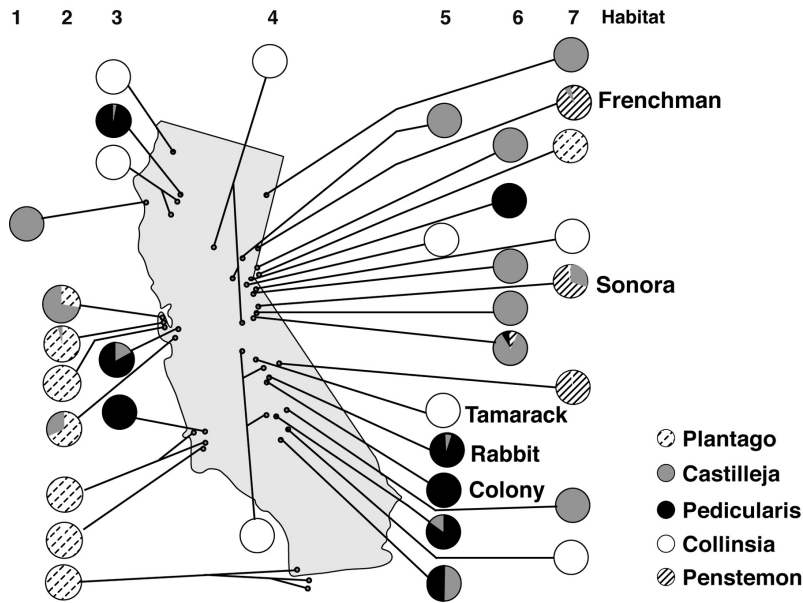


Fig. 1. Diet of *Euphydryas editha* in California. Each pie-diagram shows the proportion of eggs laid by a butterfly population on the different host genera in a single year between 1968 and 2004. Vertical columns represent different habitat types.

arises that gene flow is restricted between groups on different hosts that are subjected to divergent natural selection for host adaptations (Berlocher & Feder 2002). Therefore, studies of genetic differentiation between insects using different hosts may illuminate the mechanics of plant–insect interaction and help us to understand how insects become distributed across plants as they are. In keeping with the organization of this paper, we here describe such effects at the within-habitat-patch scale and reserve discussion of the regional scale for later.

Wee (2004 and unpubl. data) performed AFLP nuclear DNA analyses of within-site host-associated genetic differentiation among individual checkerspot butterflies. Three analyses were performed, two in populations of *E. editha* and one in a population of *Euphydryas aurinia*. Three very different results were obtained. The first result was no effect. At the Sonora junction population of *E. editha* (see Fig. 1 for location) there was no trend at all for genetic differentiation between larvae from eggs naturally laid on *Penstemon* and those from *Castilleja*. This was a young population, naturally extinct in the mid-1990s and naturally recolonized two or three years before our sample was taken. Our interpretation is that the same set of immigrants or their immediate offspring had colonized both hosts.

The second result was a differentiation in mean genotype. Larvae of *E. aurinia* found on *Succisa* and *Lonicera* at the same site differed significantly from each other. When the data were depicted on a NMDS plot showing the first two principal components of the genetic variation, the differences between sympatric larvae on the two hosts appeared to be in the same direction as differences among populations monophagous on the same two hosts. However, the host-associated differentiation within the site was much less than among allopatric populations, and host affiliation explained a much smaller proportion of genetic variance sympatrically than allopatrically. A possible interpretation is that gene flow between insects on different hosts was restricted, and had been greater when those hosts were used sympatrically than when they were used allopatrically.

The third and most puzzling result came from a population of *E. editha* at a study site (T-junction) where *Pedicularis* and *Castilleja* were both used as oviposition hosts. There was no difference between larvae from the two hosts in mean genotype but a significant difference in genetic variance. Larvae developing on *Castilleja* from eggs naturally laid on this host were significantly more different from each other than larvae from *Pedicularis* at the same site. Mean

heterozygosity was estimated as 0.137 (S.E. = 0.007) on *Castilleja* and 0.119 (S.E. = 0.007) on *Pedicularis*. The difference was significant at $p < 0.001$, using a Mann-Whitney U -test. This would perhaps be unsurprising if there were effectively two butterfly species at the site, each one specific to a single host. However, all butterflies captured at the site accepted both hosts readily. Oviposition preference trials performed on field-caught females at a site 2 km from the T-junction in the same metapopulation (Rabbit Meadow) found very weak discrimination between *Pedicularis* and *Castilleja* (Singer 1983). Almost half the insects (25 out of 54) showed no preference at all between these hosts. Therefore, it does not seem likely that we are dealing with two cryptic species, each highly host-specific. So, what could cause the genetic difference between larvae collected on the two hosts? At present, the only cause we can imagine is differential mortality of larvae in the ten days between egg hatch and time of sampling.

In our present state of knowledge, the diversity of associations between host use and genotype at local scale warns us how little we really know. We hope that further work will enable us to use genetic data to understand the interacting roles of ecological and evolutionary factors in producing spatial patterns of insects across hosts.

Checkerspot–host associations at the metapopulation scale

Granted the arguments we've made about insect distribution and host isolation, it should be no surprise that as soon as we scale up from individual hosts to patches of host plants we find that the relationship between host isolation and insect density is reversed. While isolated plants were more likely to be attacked than members of groups (Rausher *et al.* 1981), isolated populations of the hosts of *Melitaea cinxia* had lower occupancy than well-connected patches, as expected from general metapopulation dynamics (Hanski 1999). The existence of these conflicting trends at different scales makes it unsurprising that, in some analyses, the overall relationship between host density and insect density does not

reach significance (Hanski & Meyke 2005).

Movement of checkerspot butterflies among habitat patches is quite viscous (Ehrlich 1961) and is influenced by the composition of the plant community in those patches as well as by the composition of the matrix separating the patches (Ricketts 2001). Conspecific density may also be important, though effects of density seen in field experiments (Kuussaari *et al.* 1996) were opposite in direction from those in large-cage experiments at higher mean densities (Enfjall & Leimar 2005). Kuussaari *et al.* (1996) introduced *Melitaea cinxia* at different densities and showed that high nectar availability had a positive influence on immigration and a negative influence on emigration. Host plants are just as important. When a butterfly uses two or more different hosts and when habitat patches differ in their host composition the opportunity arises for complex interactions between host preferences and insect population dynamics on different hosts. We begin by considering the metapopulation of *M. cinxia* in Åland (Finland) that may be close to evolutionary equilibrium and then examine the metapopulation of *E. editha* at Rabbit Meadow where evolutionary disequilibrium induced by human habitat manipulation has generated wonderfully complex spatial effects resulting from the fact that the insects failed to prefer the host species on which fitness was highest.

The case of *M. cinxia* in Åland: metapopulation dynamics cause spatial variation of host-bias in patch colonization

The diet of *M. cinxia* in Åland comprised two host species, *Veronica spicata* and *Plantago lanceolata* (Kuussaari *et al.* 2000). Some habitat patches contained only *Plantago lanceolata*, some contained both hosts. Local butterfly populations are extinction-prone and the entire system has persisted as a result of a dynamic balance between local extinctions and colonizations (Hanski 1999). Because the extinctions were not generally caused by reductions of host density, there was a substantial supply of 'empty' habitat patches containing host plants. These patches were available for colonization. Patterns of patch

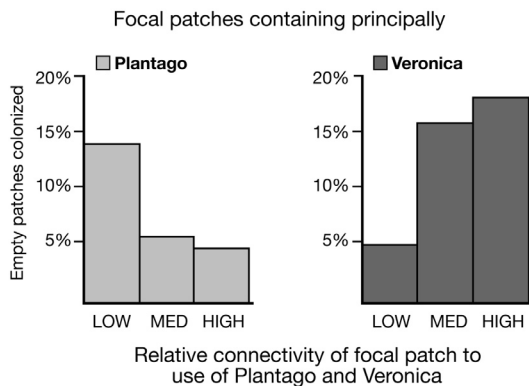


Fig. 2. Colonization rates by *Melitaea cinxia* of habitat patches containing mostly *Veronica* or mostly *Plantago* as a function of the relative connectivity of the patch to larvae found on the two hosts in previous years. A patch with “high” relative connectivity was well-connected to larvae found on *Veronica* and poorly connected to larvae found on *Plantago*.

occupancy and host plant use by larvae were known from extensive surveys performed each year (Nieminen *et al.* 2004).

Genetic variation existed among insects in the different patch networks in the preference of ovipositing adults for the two host species (Kuussaari *et al.* 2000). The most obvious effect of this variation was on electivity, the proportional use of each host as a function of its relative abundance in the habitat patch. For example, in patch networks where *Veronica* was preferred in behavioral tests using ovipositing adults, the proportion of larvae found on *Veronica* was higher than expected from the relative abundance of *Veronica* and *Plantago*. Hanski and Singer (2001) investigated the role that this preference variation might play in patch colonization dynamics. The probability that a patch containing the host *Veronica* would be colonized should increase with increasing preference for *Veronica* of butterflies that encounter the patch. So, colonization of *Veronica* patches should be high in patch networks where *Veronica* is generally preferred. Hanski and Singer (2001) were not able to measure preference directly in the several hundred patches they studied, so they used a surrogate: the relative connectivity of a focal patch to larvae previously found on each of the two hosts. Hence, Hanski and Singer (2001) reasoned that a patch with high connectivity to larvae found on *Veronica* and low connectivity to

larvae found on *Plantago* should be encountered mostly by *Veronica*-preferring butterflies. Indeed, such a patch was likely to be colonized if it contained mostly *Veronica* and unlikely to be colonized if it contained mostly *Plantago* (Fig. 2).

What drives this effect of host-specific connectivity on colonization? A patch that contains *Plantago* may remain empty either because it is not encountered by butterflies that readily oviposit on *Plantago* or because the plants in that patch are resistant to attack, i.e., not very acceptable to ovipositing *M. cinxia* in general. So the effects on colonization and electivity could be driven by variation among patches in the insects and/or in the plants. Hanski and Singer (2001), van Nouhuys *et al.* (2003) and M. C. Singer and S. van Nouhuys (unpubl. data) performed field experiments comparing both host plants and butterfly larvae in two patch types:

1. patches where both host species were used about equally and where both were about equally abundant, in other words, where the relative use of the two species could be simply predicted from their relative abundance,
2. patches where *Plantago* was used rarely or not at all and where *Veronica* received a much higher proportion of *M. cinxia* eggs than predicted from the relative abundance of the two hosts.

The results of these field trials were that both plant species were more acceptable to ovipositing butterflies in patches of type 1 than in type 2 (M. C. Singer unpubl. data). *Plantago* in patch type 2, despite receiving no natural eggs in the year of study, was acceptable to insects that preferred this species. These unused *Plantago* also supported good survival of eggs and larvae after we forced butterflies to lay on them in the field (Hanski & Singer 2001). There was no difference between insects sampled from the different patch types in the physiological ability of larvae to grow and survive on the two hosts (van Nouhuys *et al.* 2003). By elimination of other causes, we concluded that the difference between the patch types in electivity was brought about by a difference in butterfly preference. It was not caused by differences in larval performance, host accepta-

bility for oviposition or host suitability for larval development (Kuussaari *et al.* 2000, Hanski & Singer 2001). Therefore, the principal cause of the metapopulation-level effect, spatially variable host-biased colonization, was identified as genetic variation of butterfly preference.

The case of *E. editha* at Rabbit Meadow: metapopulation dynamics generated by anthropogenic evolutionary disequilibrium

Logging by the U.S. Forest Service between 1967 and 1982 created a series of habitat patches of a novel type that were available for colonization by *E. editha*. In these patches the locally-traditional host of the insects, *Pedicularis*, had been killed because it is a hemiparasite on trees. At the same time a second plant, the ubiquitous *Collinsia*, was rendered available to the insects because its lifespan was extended by the fertilization that followed the logging and burning of trash (Singer 1983, Moore 1989, Boughton 1999). In undisturbed patches, classified in previous descriptions as ‘outcrop’ patches because they often contained boulders, *Pedicularis* was still available and oviposition on *Collinsia* resulted in frequent death of offspring from host senescence (Moore 1989, Boughton 1999). Consequently, natural selection favored oviposition on *Collinsia* in clearings and avoidance of this host in ‘outcrops’ (Singer & Thomas 1996). The butterflies did indeed incorporate *Collinsia* into their diet in clearings. The first clearing had been colonized before our studies began in 1979 and all the large clearings in the patch network were occupied by 1984. However, most butterflies that used the novel host retained preferences for their traditional host and traditional habitat. In the early part of our study most insects that developed in the clearings from eggs laid on *Collinsia* nonetheless preferred to oviposit on *Pedicularis* (Singer 1983, Singer *et al.* 1992, Singer & Thomas 1996). Habitat preferences were studied by Boughton (2000), who found that both male and female butterflies were more likely to emigrate from clearing than from outcrop patches. The insects entered patches of different type at the same rate but left them at different rates, pre-

sumably because they needed to enter a patch to assess its quality.

Reversible source-sink relationships between populations in patches with different hosts

Despite a suite of maladaptations to the clearing habitat type and host plant (Parmesan *et al.* 1995, Singer 2003), the Rabbit Meadow *E. editha* achieved much higher mean fitness and higher densities in the clearings than in the undisturbed outcrop habitat patches (Singer & Thomas 1996, Thomas *et al.* 1996). The fact that fitness was highest in the habitat type that was less preferred was almost certainly an artifact of anthropogenic intervention; the system was not at evolutionary equilibrium. Butterflies preferentially emigrated from clearings and oviposited on *Pedicularis* in the nearby outcrop habitats, causing strong intraspecific competition on that host (Thomas *et al.* 1996, Boughton 1999, 2000, cf. Tschamtkke *et al.* 2005). Two statistically-significant metapopulation-level effects were generated among outcrop patches as a result of the flow of insects out of disturbed areas. With increasing isolation from insects in clearings, the density of larvae in outcrops declined (Thomas *et al.* 1996) and the strength of oviposition preference for the traditional host increased (Singer & Thomas 1996). Confirmation that these correlations were driven by biased migration came after the clearing populations were all exterminated by a frost that killed their hosts in June 1992. In 1993–1994 the association between spatial position of a patch and larval density had disappeared completely, as had the interpatch variation of oviposition preference.

Boughton (1999) studied colonization of empty patches of both types after the clearing populations had been extirpated. He found that the rate of colonization of empty outcrop patches by oviposition on *Pedicularis* was > 100 times greater than the rate of colonization of empty clearing patches by oviposition on *Collinsia*. This was due partly to host preference for *Pedicularis* and partly to a unidirectional phenological barrier. Insects developing in clearings grew faster and emerged ten days earlier than those developing in outcrops. In most years this rapid devel-

opment was necessary for insects to oviposit in clearings early enough for their larvae to survive to diapause before the annual hosts underwent senescence. Insects developing in clearings could successfully colonize either clearings or outcrops. Those developing in outcrops could normally colonize only outcrops. Boughton's (1999) conclusion was that the system had alternative stable states. The first was the state that persisted through the 1980s, with high densities in clearings, clearings acting as sources and outcrops as apparent sinks or 'pseudosinks'. (A pseudosink is a patch that is a net importer of individuals but that does not go extinct if immigration is cut off; Watkinson & Sutherland 1995.) The second stable state was observed from 1992 to 1995 and again from 1999–2004. This is the state in which densities were highest in outcrops and clearings were empty of larvae, though butterflies were seen moving through them. Outcrops were sources and clearings were true sinks.

Patch size and density: effects of scale on distribution of insects between high-ranked and low-ranked hosts

Unlogged 'outcrop' patches in the Rabbit metapopulation contained both hosts, *Pedicularis* and *Collinsia*. *Collinsia* was much the more abundant, occupying about 15% of ground cover, compared with < 4% for *Pedicularis* (Parmesan *et al.* 1995). Each year we have found more than a thousand egg clusters of *E. editha* on *Pedicularis* in these outcrops, but in no year have we found more than a single egg cluster on *Collinsia* in outcrops, even in years when larval density on *Collinsia* in clearings was ten times higher than density on *Pedicularis* in outcrops. We performed an experiment to ask whether the near-absence of oviposition on outcrop *Collinsia* reflected its reduced acceptability to ovipositing butterflies compared to clearing *Collinsia* that supported high offspring survival. In a series of paired tests we found a non-significant trend for outcrop *Collinsia* to be more acceptable after alighting than clearing *Collinsias* (Thomas & Singer 1998). Therefore, we conclude that at the within-patch scale the restriction of oviposition to *Pedicularis* reflected the combination

of pre-alighting and post-alighting preferences for *Pedicularis* over *Collinsia*. *Pedicularis* was visually preferred from a distance by all insects tested (Parmesan *et al.* 1995), chemically preferred on contact by a majority (Singer 1983, Singer & Thomas 1996) and physically preferred by insects that accepted both hosts chemically (Singer 2003).

At the within-patch scale, in outcrop patches, the distribution of insects between the preferred host, *Pedicularis*, and the less-preferred host, *Collinsia*, was explicable on the sole basis of insect preferences. Insects in general preferred *Pedicularis* and laid eggs on that host. As we move to higher scales we might expect a gradually reduced role for insect behaviour and an increased role for population dynamics as causes of the distribution of insects between the two hosts. The relationships between patch size and larval density fit this prediction very well. Small clearings with *Collinsia* were not colonized and larval densities in occupied clearings were strongly positively correlated with clearing size (Thomas & Singer 1998). In contrast, the higher risk of attack to isolated *Pedicularis* plants at this same site (Rausher *et al.* 1981) could reasonably be described as an increase in larval density at the smallest patch sizes, the opposite of the trend on *Collinsia*. So, during the decade of the 1980s, there were opposite effects of host identity on insect density at different patch sizes. At small patch sizes insects were much denser on *Pedicularis* than on *Collinsia*, while at large patch sizes (2–3 ha), they were much denser on *Collinsia* than on *Pedicularis*. At the scale of small patches the distribution of insects among hosts was still dominated by preference, as it was within the outcrop patches. At the scale of the large patch, the dominant effect was the higher survival of larvae on *Collinsia* in clearings than on *Pedicularis* in outcrops (Singer 1983, Boughton 1999).

A possible reason for the failure of butterflies to colonize small clearings is a systematic relationship between clearing size and *Collinsia* quality. However, experiments failed to reveal any such relationship (Thomas & Singer 1998), just as they had failed to find outcrop *Collinsia* inferior to clearing *Collinsia*. In contrast, the known behaviour of the butterflies does predict that small clearings should be empty. As it

searches for its oviposition site, a butterfly that prefers *Pedicularis* over *Collinsia* will reach the motivational state at which it would accept *Pedicularis* before it reaches the state at which it would accept *Collinsia*. In order to oviposit on *Collinsia*, such an insect must search for a prolonged period without finding *Pedicularis*. This is most likely to occur in a large clearing patch (recall that *Pedicularis* had been killed by logging and was absent from clearings). The high butterfly densities in large patches of *Collinsia* were achieved because insects in those patches failed to find *Pedicularis* in prolonged searches and thereby reached the high motivation levels at which they would accept *Collinsia*. Freshly-caught insects in a large patch of *Collinsia* were shown to be operating at higher mean levels of oviposition motivation than those in an adjacent patch of *Pedicularis* (Singer *et al.* 1992).

We have argued that the difference between the two host species at Rabbit in the patch size/density relation was caused principally by a general preference for *Pedicularis*. If this is correct, the tendency for small patches of *Collinsia* to be unoccupied should disappear in a metapopulation where *Collinsia* is the preferred host. It does! At Tamarack Ridge, 50 km north of Rabbit Meadow, *Collinsia* is the preferred and traditional host. There was no trend at this site for low density in small patches, and the overall patch size/density relationship differed significantly from that for the same host species at Rabbit (Singer & Hanski 2004). This result makes us wonder how well the beetles studied by Kareiva (1985) liked their host, since they consistently emigrated from small patches and only remained in large ones.

So, as scale increases host preferences become less important. But they are not irrelevant. At the metapopulation level, host preferences almost certainly affect the decision to emigrate (Thomas & Singer 1987). These authors observed that butterflies without preference between two host species were more likely to leave their current habitat patch than those actively preferring the host used in that patch. The presence of a preferred host seemed to retain the insects in the patch. Once emigration has occurred, the insect is faced with the problem of choosing a new patch in which to reside and reproduce. There

are clear effects of preference on choice of patch into which to immigrate (Hanski & Singer 2001, *see above*).

Checkerspot–host associations at the regional scale

Both *E. editha* in California and *Euphydryas aurinia* in Europe show a pattern in which only a single host genus is used over more than half the species' range, with an explosion of diet variability over a small portion of the range; southern France in the case of *E. aurinia* and California in the case of *E. editha*. The pattern for *E. editha* in California is shown in Fig. 1, in which each pie on the map represents the diet of an isolated population or an entire metapopulation. This is an update to the year 2004 of previously-published maps (Singer 2003). Some of the data are 20–30 years old but most are 1–10 years old and the map uses the latest available data for each site.

Mechanisms of spatial diversity in diet: host availability and host abundance fail to account for the spatial pattern

Mechanisms that operate among patches at the metapopulation scale should also operate at the regional scale. We would expect that the biased colonization shown in Finnish *M. cinxia* should also occur among *E. editha* populations at the scale shown in Fig. 1. The Finnish result depended on the censusing of 1600 patches each year, including empty patches. This type of intensive and systematic census of unoccupied patches has not been done for *E. editha* at the regional scale. Instead, a haphazard sample of populations has been censused in a longitudinal manner, some of them from the 1960s onwards. Although we do not know the role of biased colonization in the *E. editha* regional pattern, we do have information on the roles of variable insect preference and plant resistance as causes of the pattern shown in Fig. 1.

Part of the regional-scale variation of *E. editha* diet is a straightforward consequence of host availability, *see* Table 1. This table gives the proportion of populations at which host spe-

cies in 1, 2, 3 or 4 genera were present and the proportion of populations at which 1, 2, 3 or 4 host genera were used for oviposition. More than 60% of the sites contained only one or two host genera, so at these sites it was not possible for the diet to include 3 or 4 genera. Fewer hosts were used at most sites than were present there (Table 1). The simplest explanation might be that the insects use the most abundant hosts at each site. However, this is not the case, since any effect of host abundance on host use is slight (Table 2). *E. editha* at different sites often conspicuously choose different host species from apparently similar plant communities (Singer & Parmesan 1993, Thomas & Singer 1998). *Melitaea cinxia* does likewise (Kuussaari *et al.* 2000). When this happens, some qualitative trait of either plants or insects must be spatially variable. The next section describes experiments that asked whether plant variation and/or insect variation were responsible for an observed difference in diet of *E. editha* between two sites with similar relative abundance of potential hosts.

Mechanisms of spatial diversity in diet: spatial variability of plant resistance and insect preference combine to generate spatial variation in the plant–insect association

If we find, as we do, that the proportion of *E. editha* eggs laid on two host species varies between sites in a manner that is not explained by variation in relative abundance of the hosts, then we can describe this finding as spatially variable electivity. Singer and Parmesan (1993) devised a series of experiments to measure butterfly preference and host acceptability in two natural populations in order to understand their very different patterns of electivity. These two populations of

E. editha chose different plant species for oviposition despite the presence of apparently similar arrays of potential hosts growing at similar densities. At the time of the experiment *E. editha* at Frenchman Lake fed principally on *Penstemon rydbergii*, while those at Sonora Junction fed principally on *Collinsia parviflora*. Both *P. rydbergii* and *C. parviflora* occurred at both sites in about the same proportions and abundances. The experiments are described below.

Reciprocal transplant experiment to determine whether plant acceptability and/or insect preference differ between sites

Singer and Parmesan (1993) captured insects in the field at both sites and tested each butterfly with two plant pairs: one pair comprising a *Collinsia* and a *Penstemon* from Sonora, and one comprising a similar pair from Frenchman. After each test they discarded both the insects and the two plant pairs, and started afresh. This experimental design asks how insects taken from each site interact with plants from each site, in a general sense. Each insect and each plant was independently sampled from their respective populations, so data were independent. The result was that both butterflies and plants differed between the two sites. Frenchman insects always preferred *Penstemon* over *Collinsia*, regardless of the origin of the plant pair, giving no evidence that plants were different between the sites. However, the rankings produced by Sonora butterflies differed significantly, depending on the site of origin of the plant pair. Sonora insects were significantly more likely to prefer *Penstemon* over *Collinsia* when the plant pair was from Frenchman, the site where *Penstemon* was used. This suggested that, at least from the perspective of Sonora butterflies, Frenchman *Penstemon* was

Table 1. Host use compared to plant availability among 57 populations of *E. editha*.

	Number of genera of potential hosts			
	1	2	3	4
Populations (%) with <i>X</i> genera available	35	28	26	11
Populations (%) currently using <i>X</i> genera for oviposition	75	18	7	0

more acceptable than Sonora *Penstemon*, and/or that Sonora *Collinsia* was more acceptable than Frenchman *Collinsia*.

Genetic variation of insect preference

In the second experiment we offered all insects the same plant pair, the pair being one *Collinsia* and one *Penstemon*, both from the same site (Sonora). We did this in order to reveal variation that was clearly among insects, not among plants. When using lab-raised insects we fed all the larvae *Collinsia* and avoided testing sibs, in order to maintain independence of data points. Whether we used field-caught insects or lab-raised insects we found a significant difference in preference between insects from the two sites, in the direction that would contribute to the observed difference in diet. We concluded that genetic variation of oviposition preference among insect populations was at least part of the mechanism producing spatial variation of electivity.

Genetic variation of plant acceptability

The third experiment used plant pairs that were conspecific rather than heterospecific. Once again, each insect and plant pair were used only once to generate the dataset. Each plant pair comprised a *Penstemon rydbergii* from Frenchman and one from Sonora. Butterflies from both sites preferred the plants from Frenchman, whether the plant pairs comprised freshly-transplanted plants from the field or plants grown from seed in common soil.

The conclusion from these three experiments is that both plant and insect genetic variation contributed substantially to the spatial pattern of plant–insect association (Fig. 1). In the early

1990s *Penstemon* was virtually excluded from the diet at Sonora (we found only one egg cluster on it) partly because the local *Penstemon* population was genetically unacceptable, and partly because the local butterfly population was genetically *Collinsia*-preferring. Neither of these effects alone would have sufficed (Singer & Parmesan 1993): if Sonora butterflies were transplanted to Frenchman, *Penstemon* would instantly become a major host. And, indeed, *Penstemon* has become a major host at Sonora in 2003–2004, subsequent to a natural extinction and recolonization of the butterfly population (Fig. 1).

Diet correlates of genetic differentiation among populations

Many authors have asked to what extent the use of different hosts by different populations is accompanied by genetic differentiation among those populations, either genome-wide or restricted to traits involved in host adaptation. Sometimes these questions are asked in the interest of understanding host-associated speciation (Berlocher & Feder 2002). Other studies have been more concentrated on using diversity of diet to study evolution of resource use or coevolution (Thompson 1997, 1999, Thompson & Cunningham 2002). Whatever the motivation for the study, the data may illuminate the mechanics of plant–insect interaction and help us to understand how insects become distributed across plants as they are.

Working at the “regional” scale, Wee (2004: fig. 2) submitted a set of 30 *E. editha* populations to AFLP analysis to look for associations between diet and genetic differentiation at a scale of approximately 1000 km × 300 km. The original aim was to ask what effects diet might have on gene flow and how the effects of diet dif-

Table 2. Host preference and plant abundance among 57 populations of *E. editha*.

Populations (%) where the most-preferred host is	most abundant species	least abundant species	tied abundance	no choice
	35	21	9	35

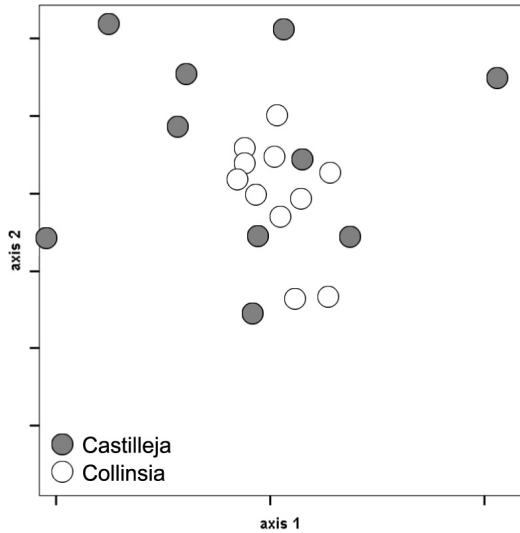


Fig. 3. NMDS (non-metric dimensional scaling) depicting relatedness of populations of *Euphydryas editha* using *Castilleja* subgenus *castilleja* (grey dots) and *Collinsia* (white dots).

ferences might compare to effects of geographic separation. We intended to do this by examining the isolation by distance relationship (IBD) if one existed and by then asking whether residuals from this relationship could be explained on the basis of diet similarity or difference. These residuals would represent pairs of populations that were either more closely-related than expected from their geographic separation, or less related than expected on this basis. A possible scenario would be that populations in the first category would tend to share their principal host while populations in the second category would not. Alas, this approach only seemed reasonable until we obtained the results. Although overall isolation by distance was significant ($r = 0.55$, $p < 0.001$) it was so heterogeneous among hosts as to question our approach of seeking residuals from some 'general' IBD relationship. Ten populations feeding on *Castilleja* subgenus *castilleja* had strong IBD ($r = 0.7$, $p < 0.001$) while 12 populations on *Collinsia* had no significant IBD ($r = 0.16$, $p = 0.15$). The *Collinsia*-feeding populations were all closely-related to each other, tightly clustered on the genetic map. The *Castilleja*-feeding populations were widely scattered on the same map (Fig. 3) in an odd evocation of the pattern found at local scale at the T-junction

site (cf. *Genetic correlates of within-site diet variation in host association*, above).

These genetic patterns, with their apparent host-specific isolation by distance relationships, may tell us something about the history of colonization of the different hosts (cf. Peterson & Denno 1998). An mtDNA analysis (Radtkey & Singer 1995) showed that the population of *E. editha* most closely related to its sympatric congener, *E. chalcedona*, fed on *Castilleja* subgenus *castilleja*, as did the population of *E. chalcedona* used in the analysis. There is a suggestion in this result that *Castilleja* might be the original host of *E. editha*. It is more likely to be so than *Collinsia*, which is not known to be the principal host of any *E. chalcedona* population, or indeed the principal host of any other butterfly. If *Castilleja* were the original host of *E. editha*, then the high genetic diversity and strong IBD among populations using it might be explained on the basis of an extended time period available for diversification, relative to populations using the more recently-acquired *Collinsia*. It is logical that the genetic clustering of *Collinsia*-feeding populations reflects a single recent acquisition of this host and the subsequent geographic spread of *Collinsia*-adapted insects by the process of preference-biased colonization discussed above. However, in order to interpret these genetic patterns with confidence we will need to know the extent to which differentiation estimated from AFLP analysis reflects effects of restricted gene flow or of selection and hitch-hiking (references in Berlocher & Feder 2002).

The "species" level: how do we decide when to call our study insects 'conspecific'?

When apparently conspecific insects occur on different hosts, individuals sampled from the same host species are often more closely-related than those sampled from different hosts. This is the case for both *E. editha* and *E. aurinia* (Wee 2004). So how do we justify describing Fig. 1 as showing a single insect species using different host genera at different sites? Why don't we call it a series of species, each associated with a particular host? Biologists are less and less in

accord about how to define ‘species’ and about whether host affiliation should play a role in the delineation of species or subspecies (Mallet 2001). More and more ‘oligophagous’ species turn out to comprise genetically distinguishable sets of populations associated with particular hosts (Hebert *et al.* 2004). It often isn’t clear to what extent this genetic differentiation results from past history or ongoing processes such as selection and drift. Neither is it clear at what point along the continuum of increasing host-associated genetic differentiation we should switch from describing a set of populations as a single oligophagous species to calling it a set of monophagous species. The manner in which this determination is made is more than simply cosmetic, it affects the way in which the study is perceived and the context in which it is apparently relevant.

In previous descriptions of our work on host relationships we have rather casually asserted that *E. editha* is an oligophagous species with geographical variation of both host use and diet breadth. The system was described in this manner for a constellation of reasons:

1. There are no obvious morphological correlates of diet.
2. Mating does not occur in association with host plants, in the sense that adults do not seek hosts on which to mate (Wee 2004).
3. Insects from populations adapted to different hosts mate readily and produce viable offspring (Singer *et al.* 1991). F2 crosses and backcrosses are also viable.
4. Two independent episodes of rapid evolution of oviposition preference have been observed over only 6–10 generations (Singer *et al.* 1993). Each has involved a phase during which a single population contained insects preferring different host genera. Strongly different oviposition preferences have been observed among siblings derived from natural matings in the field.
5. Population differentiation in allozymes was not clearly related to diet (Baughman *et al.* 1990).
6. A gene tree for mtDNA COI revealed no host-associated genetic patterns among contemporary populations, though a historical

coalescence model did uncover significant pattern (Radtkey & Singer 1995).

The genetic analyses described above have shown stronger host-association than previous genetic work on checkerspot but still do not lead us to suggest classifying the insects as more than one species. The reasons for this lie in the nature of the genetic patterns themselves, such as the pattern in Fig. 3, which shows greater genetic diversity on one host than on another, rather than the strong difference in mean genotype on different hosts that might be expected from a pair of host-associated cryptic species.

Summary

When flying adult herbivorous insects choose hosts for their sedentary larvae the nature of the in-flight search will generate spatial patterns of plant–insect association. We describe how the distribution of insect eggs among clumped and isolated plants might depend on the oviposition search. When search is initiated at random with respect to local host density, isolated plants are disproportionately attacked. We describe observations in which this process interacted with host preference when two host species were present, one generally preferred. Densities on the preferred host were highest in the smallest ‘patches’ which were isolated individuals and lower in larger patches consisting of groups of plants. Densities on the less-preferred host were zero in small patches and increased with patch area above a minimum size for the patch to be occupied. So, at small patch size, densities were higher on the preferred host while at large patch sizes (2–3 ha) densities were higher on the less-preferred host, because survival on this host was high. As scale increased, the role of insect behavior in generating spatial pattern was diminished and that of population dynamics was increased.

Moving up to a larger spatial scale, where habitat patches contained different hosts, preference-biased colonization and host-associated population growth generated metapopulation-level effects. In *Melitaea cinxia*, colonization rates of empty patches depended on the match between host composition of the patches and

the oviposition preferences of locally-migrating insects. In *Euphydryas editha*, the flow of insects among patches where different hosts were used rendered both insect density and host preference in one patch type dependent on isolation from the other patch type.

At the regional scale we summarize work showing that when one insect species used different host species at different sites, this spatial pattern emerged from a combination of genetic variation of plant acceptability to insects and genetic variation of insect preference for particular plants. We also present data on host-associated genetic differentiation of butterflies both within sites and at the regional scale. In *E. editha* isolation by distance is host-specific. These data carry implications about the history of host acquisition by the butterfly and suggest that biased colonization may have effects at scales of hundreds of km, in addition to its known impact at the metapopulation level.

Acknowledgments

We are grateful to the organizers of the workshop: Johan Kotze and Tomas Roslin. Also to Deepa Agashe, Davy Boughton, Marie Butcher, Paul Ehrlich, Ilkka Hanski, Sara Hawkins, Duncan Mackay, John Mathews, Carolyn McBride, Camille Parmesan, Rob Plowes, Chris Thomas, Saskya van Nouhuys and Niklas Wahlberg.

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