

Phenology — how time creates spatial structure in endophagous insect populations

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Received 30 Dec. 2004, revised version received 9 Mar. 2005, accepted 14 Mar. 2005

Mopper, S. 2005: Phenology — how time creates spatial structure in endophagous insect populations. — *Ann. Zool. Fennici* 42: In press.

The deme formation hypothesis predicts that short-lived insects with long-lived hosts can adapt to the traits of individual plants and form genetically differentiated sub-populations. Several life-history traits have been suggested that could predispose insects to deme formation, the most important being dispersal, feeding mode, and mating system. There is little evidence that adult dispersal ability or mating system promote fine-scale adaptation, but feeding mode appears to be important to the evolution of herbivore demes. Phenology (defined as the timing of life cycles) is now known to be individually variable and highly heritable; even a slight mismatch between an herbivore and its host can reduce egg and larval survival, or isolate adults from potential mates. This is particularly critical for internally-feeding insects that are in close and continuous contact with plants. Here I argue that endophagy, combined with insect and plant variation in phenology, are important predictors of deme formation, and a driving force behind fine scale genetic structure in herbivore populations.

Introduction

Patchy resources produce genetic structure in insect populations (McCauley 1989, Whitlock 1992, Michalakis *et al.* 1993, Mopper & Strauss 1998, Singer 2005, Weisser *et al.* 2005). This structure can be caused by stochastic events like founder effects, genetic drift, and extinction, or non-random forces such as natural selection leading to adaptation. Observations that long-lived Ponderosa pine trees provided consistent and unique resource patches for insect herbivores led to the theory of adaptive deme formation (Edmunds & Alstad 1978), which predicted that populations of insect herbivores can become genetically isolated over time into demes that are

differentially adapted to the traits of individual host plants. As demes become specialized on natal hosts, performance on novel hosts should decline. Over time, adaptations to unique plant traits will produce genetic structure in insect populations at the spatial scale of individual trees.

Dispersive insects may perceive the landscape as relatively homogeneous, whereas to a sedentary species it appears patchy and discontinuous (van Nouhuys 2005). But the strength of association between insects and plants can determine landscape qualities. As host range narrows, spatial complexity increases. Host plant species can vary in quality at multiple spatial scales (Gripengberg & Roslin 2005), even within and

among individual plants (Alstad 1998, Haukioja 2005). This creates a coarse-grained, spatially heterogeneous landscape from the perspective of an insect herbivore. Despite its potential dispersive ability, a population of insects that is structured into demes adapted to individual plants inhabits a highly fragmented and heterogeneous landscape.

For demes to evolve, individual host plants must exhibit consistent phenotypic variation. Heterogeneity in defensive traits such as tannins and monoterpenes was implicated in the original hypothesis of deme formation (Edmunds & Alstad 1978), but there is little empirical evidence for a direct link between plant chemistry and local adaptation. Experimental studies of adaptive deme formation have focused more on insect than plant traits that might facilitate genetic differentiation (Rice 1983, Hanks & Denno 1994, Mopper *et al.* 1995, Alonso *et al.* 2001). The primary insect characteristics that were considered necessary for deme formation are (1) limited dispersal behavior, (2) non-diploid breeding system, and (3) sedentary feeding mode. Lack of mobility was considered essential because demic structure cannot be sustained in the presence of gene flow, thus demes should be more common in sessile insects (Hanks & Denno 1993). Insects with haplodiploid or parthenogenetic mating systems should form demes more readily than insects with diplodiploid breeding systems, because linkage disequilibrium and co-adapted gene complexes would be less disrupted by recombination (Rice 1983). And sedentary or endophagous insects that are restricted to the same location on a host cannot escape or avoid local selection pressures, thus should be more likely to evolve into demes than free-feeding insects that can switch hosts (Mopper 1996).

Several papers have reviewed the evidence for deme formation to ascertain its prevalence in natural insect populations, and to understand the mechanisms that promote fine-scale genetic structure (Hanks & Denno 1993, Mopper 1996, Boecklen & Mopper 1998, Van Zandt & Mopper 1998, Alonso *et al.* 2001, Lajeunesse & Forbes 2002). One review concluded that restricted gene flow and host plant phenotypic variation were the main forces driving demic evolution (Boecklen & Mopper 1998). A meta-analysis of pub-

lished experiments evaluated the importance of dispersal, feeding, and breeding system to the evolution of insect demes (Van Zandt & Mopper 1998). The twelve studies analyzed were about evenly divided in support or rejection of the deme formation hypothesis. There was weak evidence that mating system and feeding mode influenced demic evolution, but no evidence that adult dispersal ability mattered.

Recent reviews have examined more closely the role played by host plants in the evolution of insect demes. One study (Alonso *et al.* 2001) reiterated the original observations of Edmunds and Alstad (1978) that variation in phenotypic traits that affect herbivore performance (such as leaf characteristics and chemical composition) was a prerequisite for deme evolution. The importance of host was reinforced by a study using item response theory to evaluate local adaptation in parasite populations, including insect herbivores (Lajeunesse & Forbes 2002). This study concluded that the most important predictor of demic evolution was host range. Specifically, parasites with one or two hosts (narrow host range) were much more likely to exhibit local adaptation than parasites with multiple hosts (broad host range). This was attributed to spatial evolutionary lags because of diffuse coevolution between the parasite and the numerous traits of multiple host species. Interestingly, many local adaptation studies use broad host range parasites, which are less likely to exhibit deme formation.

Case studies: The role of the host plant in adaptive deme formation

More than 25 years after the influential paper by Edmunds and Alstad (1978), there are relatively few tests of the hypothesis in herbivorous insect populations, and the results of these studies are mixed (Table 1). Combining studies using the same insect species, and considering only experiments that conducted transfers among individual host plants, deme formation was observed in seven of the twelve species tested (Table 2). Few of the studies confirming deme formation examined the mechanisms responsible for adaptive differentiation, and this information deficit

makes it difficult to infer patterns or elucidate specific insect or plant traits that promote deme formation.

Only Komatsu and Akimoto (1995) directly tested mechanisms of plant-mediated selection. In their experiments, heterogeneity in plant

Table 1. Experiments testing adaptive deme formation in herbivorous insect populations. Multiple citations indicate independent studies of the same insect species.

Study	Insect	Feeding	Mating	Adult mobility	Plant	ADF
Rice 1983, Alstad 1998	<i>Nuculaspis californica</i>	Fixed, exterior	Hap-dip	Passive	<i>Pinus lambertiana</i> , <i>Pinus ponderosa</i>	no
Unruh & Luck 1987, Cobb & Whitham 1998	<i>Matsucoccus acalyptus</i>	Fixed, exterior	Hap-dip	Passive	<i>Pinus monophylla</i> ; <i>Pinus edulis</i>	no
Memmott <i>et al.</i> 1995	<i>Cinara cupressi</i>	Fixed, exterior	Parth.	Dispersive	<i>Cupressus lusitanica</i>	no
Kimberling & Price 1996	<i>Daktulosphaira vitifoliae</i>	Fixed, exterior	Parth.	Dispersive	<i>Vitis arizonica</i>	no
Strauss 1997	<i>Blepharida rhois</i>	Free	Diploid	Dispersive	<i>Rhus glabra</i>	no
Wainhouse & Howell 1983	<i>Cryptococcus fagisuga</i>	Fixed, exterior	Parth.	Passive	<i>Fagus sylvatica</i>	yes
Karban 1989	<i>Apterothrips seticornis</i>	Sessile	Parth.	Passive	<i>Erigeron glaucus</i>	yes
Hanks & Denno 1994	<i>Pseudaulacaspis pentagona</i>	Fixed, exterior	Hap-dip	Passive	<i>Morus alba</i>	yes
Mopper <i>et al.</i> 1995, 2000	<i>Stilbosis quadricustatella</i>	Fixed, interior	Diploid	Dispersive	<i>Quercus geminata</i>	yes
Komatsu & Akimoto 1995	<i>Tetraneura yezoensis</i>	Fixed, interior	Parth.	Winged, low vagility	<i>Ulmus davidiana</i>	yes
Stiling & Rossi 1998	<i>Asphondylia borrichiae</i>	Fixed, interior	Diploid	Dispersive	<i>Borrichia frutescens</i>	yes
S. Egan & J. Ott (unpubl. data)	<i>Belonocnema treatae</i>	Fixed, interior	Diploid	Dispersive	<i>Quercus fusiformis</i>	yes

Table 2. Studies documenting adaptive deme formation and proposed selection mechanisms.

Study	Insect	Plant	Host phenotypic variation	Selection mechanism
Wainhouse & Howell 1983	Woolly scale	Beech	yes	unknown
Karban 1989	Thrips	Seaside daisy	unknown	unknown
Hanks & Denno 1994	Armored scale	Mulberry	unknown	unknown
Mopper <i>et al.</i> 1995, 2000	Oak leafminer	Sand live oak	yes	leaf phenology
Komatsu & Akimoto 1995	Galling aphid	Japanese elm	yes	leaf phenology
Stiling & Rossi 1998	Gall midge	Sea oxeye daisy	unknown	gall size
Egan & Ott (unpubl. data)	Cynipid gall wasp	oak	yes	leaf abscission, gall size, gall development

budburst phenology produced adaptive differentiation and spatial structure in populations of a galling aphid (*Kaltenbachiella japonica*) on Japanese elm (*Ulmus davidiana* var. *japonica*). This study demonstrated that individual developing shoots varied by as much as 70 mm in length. These host phenology differences, which were consistent between years, strongly affected aphid egg-hatch phenology, which differed by as much as 20 days among individual trees. But even slight asynchrony between timing of budburst and egg hatch caused substantial aphid mortality.

In research investigating the dynamics of an oak leafminer (*Stilbosis quadricostatella*), Mopper and colleagues demonstrated that early-season leaf maturation and late-season leaf abscission of sand-live oak (*Quercus geminata*) were associated with leafminer mortality. They proposed that synchrony between leafminer and host plant phenology was an important source of spatial structure in leafminer populations, and a mechanism that facilitated local adaptation (Mopper & Simberloff 1995, Mopper *et al.* 1995, 2000). As in the Komatsu and Akimoto study (1995), there was consistent annual variation among trees in herbivore density, bud break phenology, and tendency to abscise damaged leaves prematurely.

Two experiments have demonstrated that gall size is associated with adaptive differentiation. Both the oak gall wasp (S. Egan & J. Ott unpubl. data) and the gall midge (Stiling & Rossi 1998) produced significantly larger galls on natal plants than on novel hosts. The S. Egan and J. Ott study also showed that gall development and leaf abscission rates varied between natal and novel host plants. In these studies, bud break phenology was either not measured (Stiling & Rossi 1998), or controlled for (S. Egan & J. Ott unpubl. data) so it's impossible to determine if leaf development phenology played a role in demic structure. However, links between host plant phenology and gall size and/or density have been documented in other systems (Espirito-Santo & Fernandes 1998, Yukawa 2000, Ito & Hijii 2002, Tabuchi & Amano 2003). Leaf abscission is also a phenological trait which, like gall size, is probably influenced by interactions between the genetic traits of insects and plants.

Discussion

All of the empirical evidence for adaptive deme formation occurs in insect species that have close physical contact with their host plants: four out of seven feed internally (Komatsu & Akimoto 1995, Mopper *et al.* 1995, Stiling & Rossi 1998, S. Egan & J. Ott unpubl. data), two are permanently attached to the feeding site (Hanks & Denno 1994, Wainhouse & Howell 1983), and one feeds externally but is considered highly sessile (Karban 1989). To survive such intimate proximity requires synchronization between insect and host phenological cycles. Emergence of adults, mating, and oviposition must precisely coincide with a narrow window of resource or substrate availability. Budbreak corresponds with egg deposition, hatch, and initiation of feeding by the first-instar larva, which is typically the most vulnerable stage of the life cycle (Mopper *et al.* 2000). Even late instars are vulnerable to phenological mismatches, because premature leaf abscission can prevent pupation, or lead to increased predation and desiccation (Stiling & Simberloff 1989, Stiling *et al.* 1991). Factors other than phenology, such as localized plant defenses, can have greater impacts on insects that cannot feed freely. These pressures can be important mechanisms of selection leading to locally adapted insect populations.

All of the endophagous insects tested exhibited adaptive deme formation (Komatsu & Akimoto 1995, Mopper *et al.* 1995, Stiling & Rossi 1998, S. Egan & J. Ott unpubl. data). But not all sessile insects are locally adapted. Despite close physical contact with host plants, there was no evidence for deme formation in several species of scale insect (Rice 1983, Unruh & Luck 1987, Cobb & Whitham 1993, 1998, Alstad 1998), or in the highly sessile (when feeding) grape phylloxera (Kimberling & Price 1996). This was explained by Alstad (1998), who observed that factors like genetic drift and intra-plant heterogeneity could prevent demes from forming in populations of highly sessile insects. Similarly, Gripenberg and Roslin (2005) found greater variation in quality among shoots within *Quercus robur* trees than between trees, and concluded that *Tischeria ekebladella* leafminers were unlikely to adapt to individual trees.

The role of host phenology in herbivore demic structure

It appears from a limited number of published studies that demes will evolve when variation in host phenology is coupled with endophagy (Komatsu & Akimoto 1995, Mopper *et al.* 1995, 2000). Evidence for this is suggestive but inconclusive in two studies of gall-forming insects, where gall size was greater on natal than novel trees (Stiling & Rossi 1998, S. Egan & J. Ott unpubl. data). The timing of oviposition is essential to successful gall development, which is influenced by host phenology (Stone *et al.* 2002).

Phenology is a strong selective force for several reasons. In endophagous or highly sessile insects such as leafminers, gallformers, and scale insects, mating, oviposition, larval development, and pupation must be tightly synchronized with leaf maturation and senescence to ensure survival (Faeth *et al.* 1981, Crawley & Akhteruzzaman 1988, Auerbach 1991, Hunter 1992, Komatsu & Akimoto 1995, Van Dongen *et al.* 1997). Indeed, host phenology plays an important role in many aspects of insect ecology, including host use, outbreaks, spatial structure, and seasonal variation (Russell & Louda 2004). For example, phenological synchrony between *Rhinocyllus conicus* (flower head weevil) and *Cirsium canescens* (North American thistle) significantly influenced herbivore performance, and strongly impacted the host plant (Russell & Louda 2004). Developmental synchrony with *Q. pubescens* and *Q. petraea* was decisive to the success of *Tortrix viridiana* leafroller moths (Ivashov *et al.* 2002), and a mismatch of 4.4 days between larval emergence and budburst decreased fitness of *Operophtera brumata* moths on *Quercus robur* by 50% (Tikkanen & Julkunen-Tiitto 2003). These studies demonstrate how strongly host phenology can affect herbivore populations.

Not only can phenology directly affect survival of herbivore eggs and larvae, it can indirectly affect mating success of adults. Variation in the timing of leaf production and abscission can lead to reproductive isolation as herbivores adapt to the phenological schedules of their host (Mopper 1996). Thus allochronic separation can produce reproductive isolation within populations, as it does among herbivores feeding

on different host species that are sympatrically distributed (Southwood 1978, Tauber & Tauber 1981, Strong *et al.* 1984).

Several recent studies demonstrate that phenology is under strong genetic control. For example, *Castanea sativa* (Turkish chestnut) has at least 35 different QTLs for bud flush phenology that are stable and distributed throughout the genome (Casoli *et al.* 2004). In forest trees such as *Larix*, *Picea*, *Pinus*, and *Populus*, QTL and candidate genes determine different phenological traits (Howe *et al.* 2003), and there is “extraordinary genetic polymorphism” in the phenology of hybrids of two *Quercus* species (Ivashov *et al.* 2002). Hence, phenological variation among individual hosts can create consistent mosaics of temporal selection leading to genetically structured herbivore populations.

Much more information is needed to understand the prevalence of and conditions underlying adaptive genetic structure in insect populations. Existing studies indicate that demic structure will appear in populations of endophagous insects that feed on host plants that exhibit individual variation in phenological traits. In contrast, host plants that show little individual variation in phenology may be unlikely to promote deme formation. Free feeding insects or those with multiple host species may also be poor candidates for demic structure. Future studies should consider this and plan accordingly. To understand the process of local adaptation and the mechanisms contributing to deme evolution, reciprocal transfers and common garden experiments should be undertaken in systems with the appropriate prerequisites. With better assessment of phenological mismatches and their consequences for herbivore survival and fecundity, we can develop models that accurately predict when and where population structure occurs.

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