Geographic mosaics of species' association: a definition and an example driven by plant–insect phenological synchrony

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Abstract. Spatial mosaics occur in both evolutionary and ecological properties of species' interactions. Studies of these patterns have facilitated description and prediction of evolutionary responses of interacting species to each other and to changing environments. We propose seeking complementary understanding of community assembly and dynamics by studying ecological and mechanistic properties of mosaics. We define "species' association mosaics" as deviations from a null model in which spatial variation in the extent to which particular species interact ecologically is explained solely by variation in their densities. In extreme deviations from the null, a focal species interacts exclusively with different partners at different sites despite similar abundances of potential partners. We investigate this type of mosaic involving the butterfly *Euphydryas editha* and its hosts, the perennial *Pedicularis semibarbata* (Psem) and the ephemeral annual *Collinsia torreyi* (Ctor). A reciprocal transplant experiment showed that the proximate, mechanistic driver of the mosaic was variation in butterfly oviposition preference: the identity of the preferred host species depended on the site of origin of the insects, not that of the plants. In contrast, the evolutionary driver was phenological asynchrony between the insects and Ctor. Censuses showed that larvae hatching from eggs laid on Ctor would have suffered significantly greater mortality from host senescence at five sites where Ctor was avoided than at two sites where it was used. These differences among sites in phenological synchrony were caused by variation in life span of Ctor. At sites where Ctor was avoided, natural selection on host preference was stabilizing because Ctor life span was too short to accommodate the development time of most larvae. At sites where Ctor was used, selection on preference was also stabilizing because larvae lacked physiological adaptation to feed on Psem. These reciprocal forces of stabilizing selection formed a mosaic maintaining spatial variation in insect host preference that was the proximate cause of the species-association mosaic. In the *Discussion*, we examine the extent to which our findings hindcast an observed anthropogenic host shift by *E. editha* from Psem to Ctor. This example shows that elucidation of species-association mosaics can facilitate understanding of community evolution and dynamics.

Key words: anthropogenic evolution; eco-evolutionary dynamics; geographic mosaic; host preference; insect–plant interactions; landscape ecology; phenological asynchrony.

INTRODUCTION

Each decade we are advised anew that better integration of ecology and evolution are occurring and will soon resolve major issues in our understanding of global change and the distribution and diversification of life forms. This may finally be coming true. Spectacular progress is being made along several routes, many documented in a recent issue of *Philosophical Transactions* devoted entirely to "eco-evolutionary dynamics" (Pelletier et al. 2009). Experimental eco-evolutionary dynamics is now facilitated by automation allowing replication at levels that were previously unheard of

(Bell and Gonzalez 2011). Here we adopt an approach that is complementary to such nicely controlled experiments—simultaneous investigation of natural patterns of spatial variation in ecological and evolutionary parameters. This approach is also capable of generating insights into eco-evolutionary dynamics, community structure (e.g., Poisot et al. 2012), and testable predictions that are useful in conservation and management (Hanski 1999, 2011, Thompson 2005).

Specifically, we are interested in spatial patterns of interaction among organisms that, given the nature of their ecological specialization at the species level (Bolnick et al. 2003, DeVictor et al. 2010), can potentially interact either with each other and/or with different partners. How can we best describe these spatial patterns? Our aim is to illuminate eco-evolutionary dynamics, so our descriptors should facilitate this

aim. Where our study species inhabit discrete habitats, their patterns of presence/absence and abundance across a landscape might be described as geographic mosaics of species' occurrence, from which we can deduce the potential for those species to interact at each site. Overlaid on this pattern of species' distribution and abundance we might detect geographic mosaics of species' association, mosaics characterized by the extent to which these potential ecological interactions are realized (for example the extent to which potential competitors actually compete or the extent to which an exploiter species utilizes different populations of a particular victim species to which it is exposed). Our interest in such "species' association mosaics" is motivated by our repeated observations that spatial variation in the extent to which particular species interacted ecologically could not be predicted from spatial variation in their relative abundances (Singer and Parmesan 1993, Kuussaari et al. 2000, Hanski and Singer 2001, Olivieri et al. 2008). Accordingly, we suggest that a species' association mosaic be measured in terms of deviations from a null expectation in which species do associate according to their availabilities to each other (cf. "electivity" in Ivlev 1961). In the null scenario the proportion of an exploiter species' diet represented by prey species A would vary with the proportion of available prey that were species A. This null situation would rarely, if ever, occur in nature. For example, if prey species B were everywhere preferred over A, then the exploiter's use of A would vary spatially with availability of B as well as that of A and an observer would perceive an association mosaic between the exploiter and victim A. Despite the rarity of the null situation, we will show that investigating deviations from it can prove instructive.

Mosaics of species' association can, in turn, both engender and respond to the well-known mosaics of evolutionary interaction encompassed by the geographic mosaic theory of coevolution (Thompson 1997, 2005, 2009, Gomulkiewicz et al. 2007), mosaics of natural selection imposed by interacting species on each other and mosaics of resulting evolutionary change. Indeed, evolutionary phenomena have been the principal focus of studies addressing geographic mosaics (Gomulkiewicz et al. 2007). Patterns of variation across landscapes in selection and in (co)evolving traits have illuminated reciprocal evolutionary interactions between interacting species, often showing that the path of coevolution has proceeded at different rates or in different directions at different sites (Brodie et al. 2002, Rudgers and Strauss 2004, Siepielski and Benkman 2004, Thompson 2005, 2009, Berenbaum and Zangerl 2006, Thompson and Fernandez 2006, Gandon et al. 2008, Hanifin et al. 2008, Lively et al. 2008, Nash et al. 2008, Chaves-Campos et al. 2011, Koskella et al. 2011, Toju 2011).

We complement this approach by illustrating how simultaneously dissecting both ecological and evolutionary traits of geographic mosaics adds to our knowledge of processes involved in community assembly and helps to predict community responses to environmental change. For brevity, we describe spatial mosaic patterns of natural selection as "selection mosaics," but we should note that "selection mosaic" has a very different formal definition in the context of the geographic mosaic theory of coevolution (GMTC; Thompson 2005). A GMTC selection mosaic exists within a pair of interacting species and is defined as spatial variation in the functions that describe how the fitness of each species depends on its own trait values as well as on the trait values of its interacting partner. Gomulkiewicz et al. (2007) describe how such a GMTC selection mosaic can exist in the absence of spatial variation in the strength or direction of natural selection and, conversely, how spatial variation of natural selection can exist in the absence of the GMTC selection mosaic. Here in contrast, we use selection mosaic more simply, to refer to the fact that natural selection acting on one or more species varies among our study sites. To illustrate the relationships between association mosaics and the class of selection mosaic that we consider here, we first describe three examples of association mosaics, and then give one scenario in which an association mosaic can exist in the absence of a selection mosaic and one in which a selection mosaic can exist in the absence of an association mosaic.

Examples of association mosaics embodying strong deviations from our null model involve garter snakes studied by Arnold (1981), crossbill finches studied by Parchman and Benkman (2008), and seed beetles studied by Fox (2006). First, the garter snakes ate slugs at some sites and not at others depending on the local presence of leeches. This was because the snakes' sensory systems did not distinguish leeches from slugs, and selection against accepting leeches caused avoidance of both slugs and leeches. Second, the crossbill finches either ate or avoided seeds of ponderosa pine depending on the local presence or absence of gray squirrels, which caused the pines to evolve defenses that rendered their seeds inaccessible to the birds (Parchman and Benkman 2008). Third, the seed beetles included the exotic tree Texas ebony in their diet at some sites and not at others depending on the local presence of the native tree palo verde. Adult beetles feeding on palo verde increased their egg size in a plastic response that improved offspring survival on this tree. By coincidence, the same increase in egg size was necessary for survival on Texas ebony, though the beetles lacked an adaptive plastic response to this exotic species. In consequence, Texas ebony was only included in the insect's diet at sites where palo verde was present.

In the crossbill and garter snake examples both selection mosaics and association mosaics exist and interact. However, the two classes of mosaic are distinguishable phenomena and can exist independently of each other. In the seed beetles (Fox 2006) an association mosaic exists in the likely absence of a

selection mosaic. There is an association mosaic because the seed beetle feeds on Texas ebony at some sites and not others, even when the plant is present at all sites. This mosaic emerges because the insect's evolved adaptation to palo verde involves plasticity that increases the ability to feed on Texas ebony. Through this plasticity the ecological association mosaic develops in the absence of any spatial variation in natural selection acting on either beetle or plants, so in the absence of a selection mosaic and without evolution of the beetle to feed on Texas ebony. Short-term changes in distribution of palo verde should rapidly alter the pattern of use of Texas ebony by the beetles. The association mosaic has the potential to cause a selection mosaic, applying selection on beetles to respond adaptively to Texas ebony wherever the plant and insect coexist. We do not know whether such a selection mosaic exists because we do not know whether the beetles are variable in the relevant traits, and we do not know whether a response to such a selection mosaic will occur. When last investigated, it had not (Fox et al. 1997).

For a converse example, a selection mosaic in the likely absence of an association mosaic, consider the study by Thompson and Cunningham (2002), who describe a selection mosaic involving a moth (*Greya*) that both pollinated and fed upon the same plant species (*Lithophragma*) at different study sites. The moth could act effectively as a parasite or as a mutualist of the plant, depending on the availability of alternate pollinators. The authors view these different relationships as generating a selection mosaic acting on both plant and moth; each species should suffer spatially variable selection on traits that affect its interaction with the other species. However, the moth was normally monophagous and fed on *Lithophragma* at all 12 study sites, so no association mosaic was documented between the moth and the plant.

These scenarios argue for complementing the traditional emphasis on evolutionary aspects of mosaics with a more mechanistic ecological, physiological, and behavioral perspective that may make its own contribution to our understanding of landscape-level events and to the prediction of community responses to environmental change. In the empirical work described here, we illustrate this approach by describing a geographic mosaic of plant–insect interaction as a species' association mosaic, investigating both its mechanistic causes and its maintenance by a selection mosaic, and asking how well these processes hindcast observed community responses to anthropogenic change.

The mosaic that we studied differs from the garter snake, crossbill, and seed beetle examples, in which the diet of an exploiter species expanded and contracted across space to include or exclude particular victims, in each case depending on the presence of a third party (leeches, squirrels, and palo verde, respectively). In our example, the diet of an exploiter switches completely from one victim to another rather than expanding and

contracting from a focal victim to include or exclude an additional victim. Our interest in this type of pattern dates back to a prior study involving the checkerspot butterfly *Euphydryas editha*, which fed on *Penstemon rydbergii* at one site and *Collinsia parviflora* at another (Singer and Parmesan 1993). This species' association mosaic was driven mechanistically by a combination of genetic variation of plant resistance and genetic variation of insect preference. At the site where the insects avoided oviposition on *Penstemon* this was partly because the local *Penstemon* was less acceptable (more resistant) than at the other site and partly because the local butterflies were more *Collinsia*-preferring (cf. Stenberg et al. 2008). This study was mechanistic and no evolutionary explanation for the pattern was sought.

The present work investigates a second, apparently independent, example in which the same exploiter species (*E. editha*) switches between two other victims in a geographic mosaic distributed across an area ~1000 × 300 km. In this case the victims are *Pedicularis semibarbata* (hereafter abbreviated as Psem) (dwarf lousewort, Orobanchaceae), and *Collinsia torreyi* (Ctor) (baby blue lips, Plantaginaceae). We expand on the prior approach by seeking both mechanistic and evolutionary causation of the mosaic, proceeding in the following sequence.

1) We document the nature and persistence of the geographic mosaic. Previously published data on our current study populations (Singer and McBride 2010) simply categorized each population as feeding on Psem or Ctor without providing data on which those diet categorizations were based. Here, we present census data gathered across decades to estimate densities of the two host plants at each site, record the numbers of insects found feeding on each species, and assess consistency over time of spatial patterns in insect diet and plant abundance.

2) We investigate the relative roles of variation in butterfly oviposition preference and host plant acceptability as mechanistic causes of the geographic mosaic. We begin with knowledge that variation of preference exists, demonstrated by testing the preferences of insects from five of our study sites, using plants from a single site (Singer and McBride 2010). We complement these published data with additional preference tests that generate a reciprocal transplant design, with insects from two sites tested on plant pairs from each site. This allows us to determine whether variation in plant acceptability contributed to the difference between sites in species' association.

3) We document variation among sites in phenological synchrony between the insects and Ctor, and in the phenological stress that would be suffered at each site by the insects, if they fed on this plant. We use the results to deduce the spatial pattern of natural selection on insect diet.

4) We assess whether intersite variation in phenological synchrony between *E. editha* and Ctor was caused by variation in life span of Ctor and/or in the timing of the insects' life cycle.

5) We ask whether understanding of the behavioral/ ecological mechanisms and selective forces currently acting in the landscape-level mosaic across hundreds of kilometers can hindcast details of an anthropogenic host shift between the same two plants undertaken by a single metapopulation of the butterfly in the 1980s across a smaller-scale mosaic measuring only 8 × 10 km.

STUDY SYSTEM

Host shifts are known to be important precursors of phylogenetic diversification in butterflies (Nylin and Janz 2009, Fordyce 2011), and Melitaeine butterflies, the group to which our study insect, *Euphydryas editha*, belongs, typically undergo frequent host shifts (Singer et al. 1993, 2008). Melitaeines, especially *Melitaea cinxia* and *E. editha*, have proven amenable to field investigations of their relationships with host plants, a topic on which considerable information has accumulated (Thomas 1986, Singer et al. 1988, Boughton 1999, Hanski 1999, Kuussaari et al. 2000, Hanski and Singer 2001, Hellmann 2002, Van Nouhuys et al. 2003, Ehrlich and Hanski 2004, McBride and Singer 2010, Singer and McBride 2010, Singer and Parmesan 2010).

E. editha is an insect of sedentary habit (Ehrlich 1961, Gilbert and Singer 1973, Harrison et al. 1988, Boughton 1999) distributed in isolated populations and metapopulations across the western United States, western Canada, and northwestern Baja California (Parmesan 1996, Singer and Wee 2005). At montane sites such as those in this study, *E. editha* has a single generation per year. Larvae diapause through late summer, fall, and winter and break diapause at snowmelt. About a month later, adults emerge. Females typically commence oviposition on day 2 or 3 after eclosion. Eggs hatch in approximately two weeks and larvae need to feed through three instars (10–20 days) before they are capable of diapausing. Host phenology is extremely important to these larvae, as is known for other butterflies (e.g., Fordyce and Nice 2003). At sites where their host plants are annuals, *E. editha* larvae risk starvation if they fail to reach third instar before their hosts senesce. A final-instar female larva can reduce this risk to her offspring by pupating earlier in development, but at the cost of reduced size and fecundity. Alternatively, she can be large, fecund, and late, in which case the risk of offspring mortality is increased. Faced with this trade-off between adult fecundity and offspring mortality the insects frequently evolve to a size at which phenological synchrony between insect and host is poor and larval mortality from host senescence is substantial (Singer and Parmesan 2010).

An *E. editha* larva feeding on a senescent plant is not necessarily doomed; even first-instar larvae have some ability to leave their natal host and search for another (Hellmann 2002), and this ability improves in succeeding instars. Nonetheless, *E. editha* larvae do frequently die from phenological asynchrony with their annual hosts (Weiss et al. 1988, Moore 1989, Thomas et al. 1996, Boughton 1999, Singer and Parmesan 2010).

Our present study is restricted to sites where *E. editha* is known to feed on either Ctor or Psem. The geographic distribution of these sites is shown in Fig. 1 (exact locations in Appendix A). While Ctor is a short-lived, nonparasitic, annual plant, Psem is a long-lived hemi-parasitic perennial, parasitizing coniferous trees. Various *Castilleja* (Orobanchaceae) are also used by populations whose principal host is Psem (Singer and Wee 2005, Singer and McBride 2010), but we have not explicitly incorporated this genus into the current study. Although Melitaeine butterflies are capable of responding more strongly to variation among individual plants than to variation among species or even genera (Singer and Lee 2000), the butterflies in the current study did treat Psem and Ctor as separate entities. For example, a butterfly that expressed a preference for Ctor over Psem would not switch to preferring Psem over Ctor when offered different individual plants (see *Results*).

Despite widespread coexistence of our two focal plants, they are currently used by the butterflies only allopatrically (i.e., by butterfly populations that are geographically isolated from each other). Previous work showed that butterfly populations using these hosts were systematically differentiated by a complex suite of host-adaptive traits including larval performance and foraging height, adult alighting bias, oviposition preference, oviposition height, and clutch size (cf. Nosil and Sandoval 2008, Singer and McBride 2010). Hybrids between insects from differently adapted populations were vigorous and fecund but showed maladaptive, intermediate phenotypes resulting in sequential fitness losses at different life-history stages, no matter which host they used (McBride and Singer 2010). Despite the existence of this extended set of genetically based differences in physiology and behavior between butterfly populations in the two host-use categories, and despite the problems faced by hybrids, we do not classify the two butterfly ecotypes as cryptic species because we detect no other sign of reproductive isolation and no host-associated component of overall genetic differentiation (McBride and Singer 2010).

METHODS

Spatial patterns of insect diet and host abundance

The butterflies are very patchily distributed across the landscape, much more so than their hosts, such that both plants are frequently abundant well beyond the borders of the butterfly populations. From the perspective of our study, the relevant host densities are those measured within the butterfly populations. We estimated these densities at each site by counting hosts in 30-cm^2 quadrats placed by pacing random numbers along line
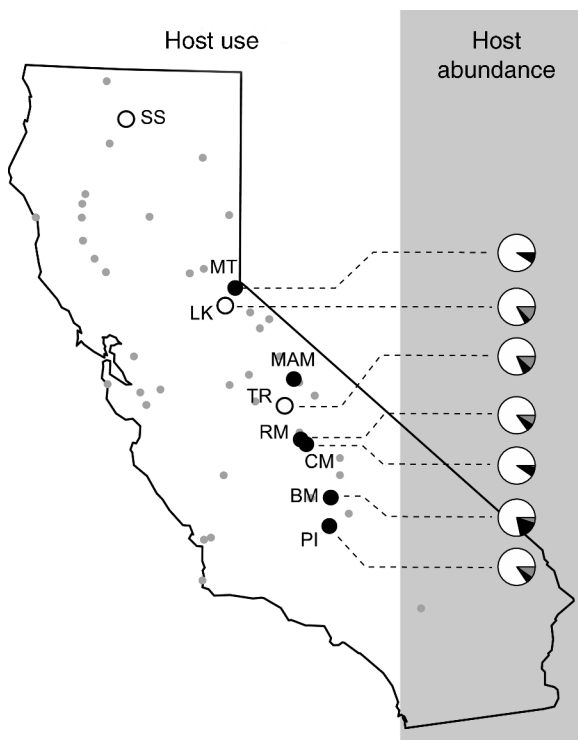
FIG. 1. Map of California, USA, illustrating a species' association mosaic involving the butterfly *Euphydryas editha* and two of its host plants at sites in open coniferous woodland between 2000 and 2500 m on the western slopes of the Sierra Nevada and Cascades (except MAM at ~3000 m and SS at 1500 m). *E. editha* populations using *Collinsia torreyi* (Ctor) or *Pedicularis semibarbata* (Psem) are indicated by open and solid circles, respectively. Sites are abbreviated as follows: SS[C], Snowman Summit; MT[P], Mount Tallac; LK[C], Leek Springs; MAM[P], Mammoth Crest; TR[C], Tamarack Ridge; RM[P], Rabbit Meadow; CM[P], Colony Meadow; BM[P], Big Meadow; PI[P], Piute Mountain. Superscripts on site names indicate diet (P, Psem; C, Ctor). *E. editha* populations with diets other than *C. torreyi* or *P. semibarbata* are indicated by gray dots. Pie charts show the relative frequency of quadrats in which only Ctor was present (open), only Psem was present (solid), or both hosts were present (gray). Quadrats without hosts are not shown.

transects. Host availability was quantified both as mean number of individuals per quadrat and as proportion of quadrats containing at least one individual. We estimated insect densities at sites where they were abundant by counting egg clutches or early instar larvae in the same quadrats used to estimate host density. Where the insects were rare, we recorded all the eggs or larvae that we could find and the numbers of host plants that we searched.

Intersite variation in insect preference and host plant acceptability

Previous work showed that variation in insect preference contributed to intersite differences in host use. In order to test whether variation in plant acceptability also contributes, we assayed oviposition preferences of field-caught insects using plant pairs (Ctor-Psem) from different origins. This was done with a bioassay in which repeated, brief (3-min) encounters were staged between the insects and each host plant in alternation (Singer et al. 1992). Behavioral responses were noted at each insect–host encounter. Insects were not allowed to oviposit, but attempts to do so were recorded as acceptances of the test host (see supplemental videos to McBride and Singer [2010] and imagine that the insect is removed from the plant after the ovipositor is extruded and pressed against the leaf). A host was recorded as preferred if it was accepted and the other host subsequently rejected (Singer et al. 1992, Singer and McBride 2010).

Intersite variation in phenological synchrony between insects and Ctor

Relative phenology of plants and insects at seven sites.—The degree of phenological synchrony between a Ctor-feeding *E. editha* larva and its host, an estimate of the "phenological stress" that the larva suffers, was measured by making synchronous recordings of larval instar and the condition of the plant on which each larva was feeding (Appendix B). Using the criteria laid out in Appendix B, we routinely observe larvae that would be classified as suffering phenological stress in our study sites where Ctor is the host (Table 1). We were interested in asking whether this phenological stress suffered by insects feeding on Ctor would differ between sites where this host is used and those where it is not. To do this, we compared sites in a way that was consistent among sites and independent of decisions made by local insects. At each study site we made simultaneous recordings of the phenological stages of local Ctor plants (regardless of whether or not they bore insects) and of local *E. editha* populations (regardless of which host they used). The phenological stage of a Ctor population was assessed by recording the proportion of plants in each of following four stages: (1) budding (plants with at least some buds yet to open); (2) blooming (plants with open flowers and no developing buds); (3) senescent (plants no longer blooming, with leaves turning red or yellow but not yet dry and brittle; these plants are edible to *E. editha* larvae; and (4) dead (inedible plants with brittle, dry leaves).

Each plant was chosen independently of others. The phenological stage of a butterfly population was likewise assessed by recording the proportion of insects found in four different stages: eggs, first-instar, second-instar, and third-instar larvae. We timed our recording at each site before the most advanced larvae had entered diapause, to get a comparison among sites of the availability of food to larvae at this critical point in their life history. We assigned scores to the phenological stages of each plant and insect censused: budding Ctor, 1; blooming, 2; senescent, 3; dead, 4; insect eggs, 1; first instar, 2; second instar, 3; third instar, 4. We calculated mean scores for each population and divided the mean score of the plants by that of contemporary insects. This generated a single number for each site, giving a rough estimate of

TABLE 1. Observed phenological stress in *Collinsia torreyi* (Ctor)-feeding sites in California, USA.

Site	Subsite	Year	Category of plants	Bud (no.)	Bloom (no.)	Senescent (no.)	Dead (no.)
TR^C	B	2009	random	1	2	34	16
			with eggs				
			with first instar	3	3†		
			with second instar	3	3	1†	
			with third instar			1	
TR^C	A	2009	random	14	28	8	2
			with eggs	1			
			with first instar	5	1†	1‡	
			with second instar		2	2†	
TR^C	A	2002	random	6	5	21	2
			with eggs	1	1‡		
			with first instar	5	5†	1‡	
			with second instar	8	5	9†	
			with third instar	2	6	10	
TR^C	A	1995	random				
			with first instar	7	2†	2‡	
			with second instar	7	6	11†	
			with third instar	1	4	13	
LK^C		2010	random	5	21	86	1
			with first instar	6	2†		
			with second instar	3	7	3†	
			with third instar			2	

Notes: The table shows the phenological stages of plants that were chosen at random or that carried insects at the given life stages. Random plant censuses are included to illustrate the extent to which the insect distributions were biased toward phenologically young plants. See Fig. 1 for site abbreviations.

† The insects would suffer moderate phenological stress according to the criteria in Appendix B.

‡ Situations of high phenological stress for the insects.

phenological stress that would be suffered by an insect population feeding on Ctor plants and choosing them at random with respect to their phenology. Higher numbers represent phenologically advanced plants relative to insects, therefore greater phenological stress for the insects. We averaged this phenological stress index across years when data were available for several years at the same site, to obtain a single mean value for each site. We then performed a *t* test on these means to compare stress indices from sites where the butterflies actually used Ctor with that for sites where they used Psem.

Absolute plant and insect phenology at two sites.—Ctor seeds germinate and *E. editha* larvae break diapause within a few days of spring snowmelt, which was synchronous in 2009 (*available online*)[5] at two of our study sites, RM^P and TR^C (superscripts indicate diet; P, Psem; C, Ctor) that are only 60 km apart and at identical elevations. We took advantage of this coincidence. Using the categories described in the previous section (budding, blooming, senescent, dead), we compared phenological stages of Ctor at these two sites at times when their chronological ages would have been the same. We also recorded phenologies of the butterfly populations at two time intervals: when adults were flying and, subsequently, when prediapause larvae were feeding. Adult insects were censused by capturing them and assigning each individual to one of four wing-wear categories, using two symptoms of normal aging. First, friction between hindwings and forewings in flight gradually removes scales from the undersides of the forewings. Second, the delicate fringe of

5 http://cdec.water.ca.gov/

black and white hairs at the wing margins is degraded during flight and disappears completely after three or four days of activity. Our four age categories were: (1) new, likely age range 0–2 active days, no visible wing wear, no scales missing from underside of forewing, hair fringes around wing margins intact; (2) young, likely age range 2–6 active days, wing margin fringes tattered, few scales missing from forewing underside; (3) middle-aged, likely age range 5–14 days, fringes completely missing, forewing underside becoming visibly shiny from loss of scales; and (4) old, likely age range 12–20 days, colors fading across all wing surfaces, wings becoming transparent.

Correlation between number of inflorescences and longevity.—Based on observations in the field at several sites, we hypothesized that the number of reproductive structures on mature Ctor plants might be an easily measured surrogate for longevity. To test this hypothesis, we recorded both the number of inflorescences (buds, flowers, and seed capsules) and the phenological condition (budding, blooming, senescent, dead) of all Ctor plants in 16 randomly placed 30-cm quadrats at site RM^P and TR^C in 2002 and 2003. Inflorescences were counted at times when plants were sufficiently mature that few new flowers would develop. Because germination is synchronized within a quadrat at snowmelt, a smaller number of inflorescences on senescent and dead plants compared with contemporary blooming and budding plants in the same quadrat indicates shorter life span for plants with fewer reproductive structures.

Intersite variation in number of inflorescences on Ctor.—We counted the number of inflorescences on

TABLE 2. Summary of recorded use of hosts *Collinsia torreyi* (Ctor) and *Pedicularis semibarbata* (Psem) by *Euphydryas editha* at nine study sites across three decades.

	Study sites								
Decade	PI[P]	BM[P]	CM[P]	RM[P]	TR[C]	MAM[P]	LK[C]	MT[P]	SS[C]
1980s	Psem	Psem	Psem	both†	Ctor				
1990s	Psem	Psem		both†		Psem	Ctor	Psem	Ctor
2000s	Psem	Psem	Psem	Psem	Ctor		Ctor	Psem	
2010			Psem	Psem	Ctor		Ctor	Psem	

Notes: Populations are listed from south to north. Detailed census data for individual years are given in Appendix C. Daggers indicate an episode of anthropogenic diet evolution described in the *Discussion*. The table shows only the use of the two hosts discussed in the paper; with the exception of CM[P] and MAM[P] populations that used Psem also used the closely related genus *Castilleja* (Orobanchaceae). Populations using Ctor were monophagous except that <5% of eggs at TR in 1986 were laid on *Veronica serpyllifolila* and *Mimulus breweri* (Singer et al. 1994).

individual Ctor plants at all eight sites in our study: five sites where the insects fed on Psem and three where they fed on Ctor. At each site, points in space were chosen by pacing random numbers along line transects. The closest plant to each point was chosen and the total number of buds, flowers, and capsules was counted. Once again, we censused at times when few new flowers would develop.

RESULTS

No relationship between insect–host association and plant densities

The geographic pattern of host use has been consistent over decades (Table 2; Appendix C) at all sites except RM[P], where the plant–insect association evolved during the 1970s and 1980s (see *Discussion*) and for which we restrict our data to the past decade. Over 99% of oviposition records at three sites (TR[C], LK[C], SS[C]) were on Ctor. At the other six sites (PI[P], BM[P], CM[P], RM[P], MAM[P], MT[P]), eggs were principally laid on Psem with none found on Ctor but variable use of *Castilleja* spp., not shown in the figures or tables.

Despite discrete differences in insect host use, we found little variation in host availability among sites

that were censused (Table 3, Fig. 1), although we anecdotally observed reduced distribution of Ctor at one Psem-feeding site, MT, in 2011. In the census data, overall proportions of quadrats containing each host species were almost identical at sites where host use differed. At Psem-using sites 9% of quadrats contained Psem and 54% contained Ctor, while at Ctor-using sites 9% contained Psem and 52% contained Ctor. Mean overall density of Psem was also virtually identical at sites where it was the host (0.096 plants/quadrat) and sites where it was not (0.099 plants/quadrat). Ctor was slightly less dense at sites where it was used (2.83 plants/quadrat) than at sites where it was not (16.4 plants/quadrat), but this difference was not quite significant (t test $P = 0.06$) and in the opposite direction from what one would expect based on insect host use.

Mechanistic cause of the mosaic: variation in plants, in insects, or in both?

Previous work showed that butterflies from Psem- and Ctor-feeding sites differed markedly in host preference when taken to a single site (RM[P]) and tested using plants from that site (Singer and McBride 2010). Insects from LK[C] and TR[C] consistently preferred Ctor over

TABLE 3. Host abundance at ecologically similar sites on the western slopes of the Sierra Nevada and Cascades (BM[P], CM[P], RM[P], TR[C], LK[C]) and on the crests of the mountain ranges (PI[P], MT[P]).

Site	Year	Quadrats searched	Mean hosts/quadrat		Proportion quadrats with host			Ratio Ctor/total hosts
			Ctor	Psem	Ctor	Psem	Both	
PI[P]	2009	37	34.2	0.11	0.57	0.03	0.05	0.997
	1986	46	34.7	0.11	0.48	0.04	0.07	0.997
BM[P]	2009	28	12.6	0.07	0.64	0.00	0.07	0.994
	1988	10	3.2	0.20	0.40	0.20	0.00	0.941
CM[P]	2009	122	14.6	0.04	0.55	0.02	0.02	0.997
	1989	36	28.9	0.06	0.42	0.06	0.00	0.998
RM[P]	2009	50	10.3	0.06	0.62	0.04	0.02	0.994
	2002	77	12.8	0.19	0.45	0.04	0.08	0.985
TR[C]	2010	20	2.2	0.05	0.75	0.00	0.05	0.978
	2009	56	2.1	0.09	0.34	0.05	0.04	0.959
	2004	25	3.5	0.12	0.40	0.04	0.08	0.967
	2003	33	2.9	0.12	0.52	0.06	0.06	0.960
	2002	38	2.1	0.11	0.34	0.03	0.08	0.952
LK[C]	2010	39	2.9	0.05	0.49	0.00	0.05	0.983
	1999	40	3.3	0.15	0.38	0.05	0.08	0.956
MT[P]	2010	20	6.0	0.05	0.50	0.05	0.00	0.992

Notes: Sites listed from south to north (superscripts in site codes indicate insect diet). See Fig. 1 for site abbreviations.
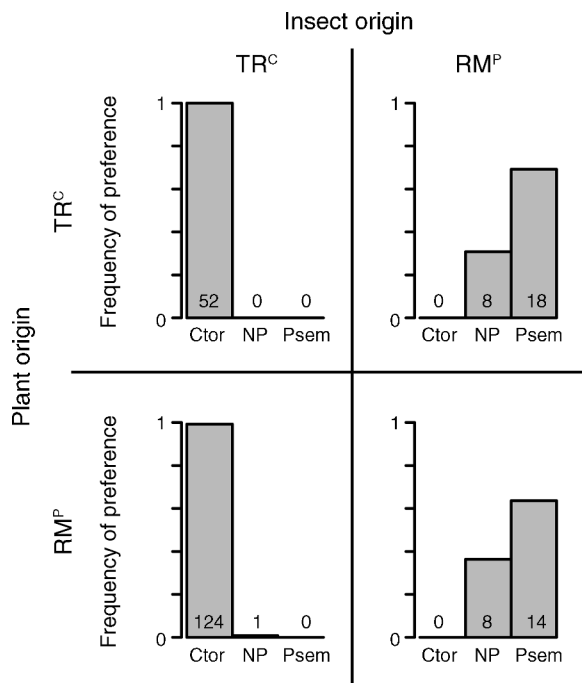
FIG. 2. Oviposition host preferences of butterflies caught in the field and tested on plants gathered either at their own site or at a different site. Each plot shows the frequency of observed preferences (*y*-axis) for Ctor, neither host (NP, no preference), or Psem. Ctor is the traditional host at TR^C, and Psem is the traditional host at RM^P. A subset of data for butterflies tested on plants from RM (two bottom panels) was also shown in Fig. 3 of Singer and McBride (2010). All data for butterflies tested on plants from TR^C (two top panels) are new. Numbers above the *x*-axes indicate sample sizes. Raw data are provided in Appendix D. See Fig. 1 for site abbreviations and superscript explanation.

Psem. Most insects from the Psem-feeding sites preferred Psem, though a substantial minority showed no preference between the two hosts. New tests are added here to form a reciprocal transplant design for sites RM^P and TR^C, allowing us to test the role of plant variation. The proportions of insects preferring to oviposit on

Ctor, preferring Psem, and without preference are shown in Fig. 2 (see also Appendix D). When Psem-using insects from Rabbit Meadow (RM^P) were tested on plants growing at Tamarack (TR^C), they showed no tendency for decreased preference for Psem, compared to tests with plants growing at their home site. Likewise, butterflies from Tamarack (TR^C) retained their unanimous preferences for Ctor whether tested at home (TR^C), on naturally growing plants at RM^P (Fig. 2), or on plants gathered at PI^P (Appendix D).

Sites vary in phenological synchrony between insects and local Ctor

Recording of plant and insect phenology across sites with the two insect–host associations revealed Ctor plants to be more mature, relative to the phenology of the insects, at five sites where Ctor was not used (PI^P, BM^P, RM^P, CM^P, MT^P), than at two sites where it was the host (LK^C, TR^C) (Table 4, Fig. 3A). Phenological stress that would result from using Ctor plants at random was significantly lower at sites where Ctor was the host (mean stress index = 0.87) than at sites where it was not used (mean = 1.61) ($P = 0.016$, *t* test comparing overall site means).

Two sites vary in absolute timing of Ctor, but not insect, phenology

The age distribution of flying butterflies at TR^C on 24 June 2009 was extremely similar to the distribution at RM^P on 25–26 June of the same year (Fig. 3B). The distribution of larval growth stages, recorded on consecutive days in July, was also similar (Fig. 3B). In contrast, phenology of the plant populations was very different between the same sites; plants growing at TR^C were less mature than their contemporaries growing at RM^P (Fig. 3B). Because snowmelt was synchronous at these two sites in 2009 and Ctor seeds germinate immediately after snowmelt, the difference between sites in plant phenology can be attributed to a difference in

TABLE 4. Survey of phenological synchrony between insects and Ctor.

Site	Date	Insects					Ctor host plants					Stress index
		Egg	First	Second	Third	Score	Bud	Bloom	Senescent	Dead	Score	
PI^P	19 Jul 2009	12	4	2	0	1.44	0	14	145	2	2.93	2.03
BM^P	18 Jul 2009	0	0	6	4	3.40	0	0	0	350	4.0	1.18
CM^P	24 Jul 2009	0	0	14	2	3.13	0	1	17	1749	3.99	1.28
RM^P	21 Jul 2010	3	8	9	2	2.45	0	0	10	1179	3.99	1.63
	14 Jul 2009	3	13	11	5	2.56	0	0	11	65	3.86	1.51
	30 Jun 2002	10	13	7	0	1.90	9	57	311	117	3.09	1.62
TR^C	22 Jul 2010	1	5	13	2	2.76	46	93	178	9	2.46	0.89
	13 Jul 2009	1	13	11	1	2.46	15	30	42	18	2.60	1.06
	12 Jul 2002	2	11	22	18	3.06	6	5	21	2	2.56	0.84
LK^C	9 Aug 2010	0	8	13	2	2.74	5	21	86	1	2.73	1.00
	22 Jul 2009	1	1	12	10	3.29	5	12	5	0	2.00	0.61
MT^P	10 Aug 2010	1	8	5	0	2.29	0	0	5	148	3.97	1.74

Notes: Scores indicate the mean life stage of insects or plants on the given date (see *Methods*). The stress index represents the maturity of plants relative to insects (plant score/insect score) and provides an estimate of the likely mortality from host senescence of larvae feeding on Ctor at each site, whether or not Ctor was actually used. See Fig. 1 for site abbreviations.
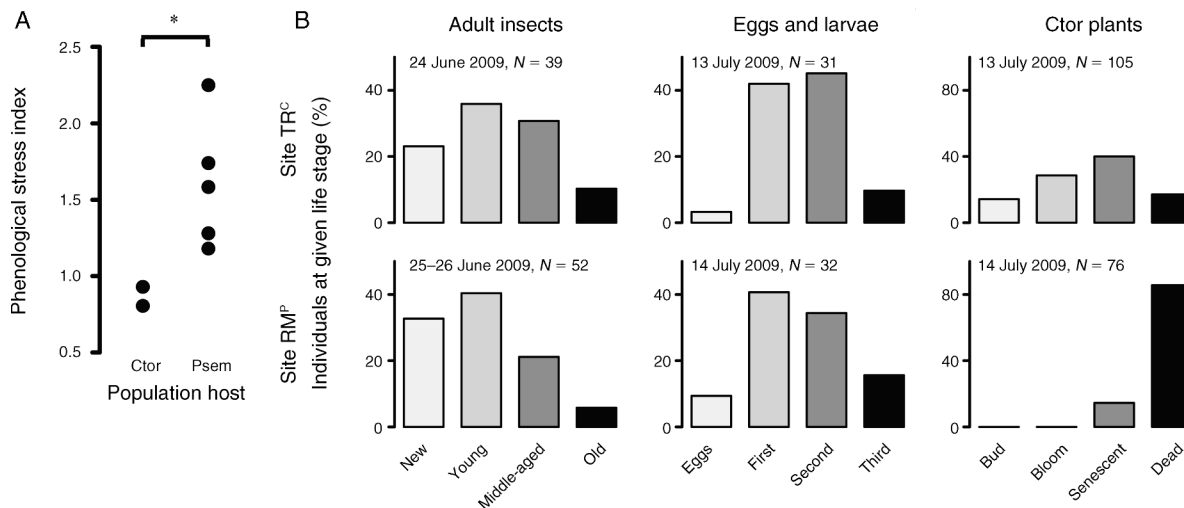
FIG. 3. (A) Visual display of indices of phenological synchrony between butterflies and Ctor, calculated in two Ctor-feeding sites and five Psem-feeding sites. These are the overall site means calculated from the "stress index" column shown for individual years in Table 4. The asterisk indicates *t* test *P* < 0.05. (B) Phenological synchrony in 2009 between a Ctor-feeding site and a Psem-feeding site with synchronous snowmelt in that year (snowmelt information from footnote 5 where site codes are bim for site RM and tmr for site TR). Older or more mature individuals are shown in darker color for both plants and insects. "First," "second," and "third" refer to larval instars. Most larvae in third instar would be able to diapause if starved; no larvae in earlier stages would survive without food. Larvae can eat senescent plants, but not dead plants. Ctor phenology differs between sites by contingency test: $\chi^2 = 40.1$, df = 1, *P* < 0.0001.

longevity, with Ctor plants living longer at TR[C] than at RM[P].

Host use is correlated with intersite variation in size, and hence longevity, of local Ctor

Ctor phenology was negatively correlated with the number of inflorescences at RM[P] and TR[C]; plants with more infloresences were phenologically less advanced and would continue to be edible to insects for longer than those with fewer infloresences (Fig. 4A; ANOVA *P* < 0.0001). Interestingly, the number of inflorescences on mature Ctor also varied among sites. Mature Ctor plants had many more inflorescences at sites where local butterflies used them as hosts (Fig. 4B, white boxes) than at sites where local butterflies used Psem instead (Fig. 4B, gray boxes; ANOVA *P* < 0.0001). This striking difference was the only obvious factor differentiating hosts growing at Ctor- and Psem-using sites. Moreover, given the association between Ctor longevity and inflorescence number observed within sites (Fig. 4A), it suggests that Ctor is longer-lived at sites where it is used as a host. Variation in Ctor life span and not in insect developmental rate is likely to be the principal driver of variation in synchrony between the butterflies and Ctor across all sites (Table 4). The detailed study of two sites (*Results: Two sites vary . . .*) is a microcosm of the larger pattern.

DISCUSSION

In the *Introduction*, we defined geographic mosaics of species' association as deviations from a null model in which strengths of interaction vary in space in ways that

can be simply predicted from variation in availability of potential partners. We present data that fit our definition of such a mosaic (Fig. 1, Table 3). Although a survey of 57 populations of *E. editha* had previously revealed a weak trend for the insect to specialize on more abundant, rather than less abundant hosts when a choice was available (Table 2 in Singer and Wee 2005), the present study found no trend for Ctor to be more abundant at sites where it was used. This pattern was consistent across decades (Tables 2 and 3; Appendix C) regardless of whether we measured abundance in terms of absolute numbers of Ctor and Psem plants, relative abundance of Ctor and Psem, or the presence/absence of each host in 30-cm quadrats (Table 3). The last is, we think, the most relevant of our measures to searching insects and is the one represented in Fig. 1.

Proximate cause of the geographic mosaic: butterfly oviposition preference

We began the current study with the knowledge that variation in oviposition preference would be at least a part of the mechanistic cause of the geographic mosaic. Prior work had shown that, when tested on local Psem and Ctor at Rabbit Meadow (RM[P]), butterflies brought from two Ctor-feeding populations (LK[C], TR[C]) and two Psem-feeding populations (PI[P], BM[P]) preferred the hosts used at their respective natal sites (Singer and McBride 2010). We also know from prior work that genetic variation among plant populations (in acceptability to the butterflies) was an essential component in the mechanistic basis of an association mosaic between *E. editha* and two other hosts (*Penstemon rydbergii* and
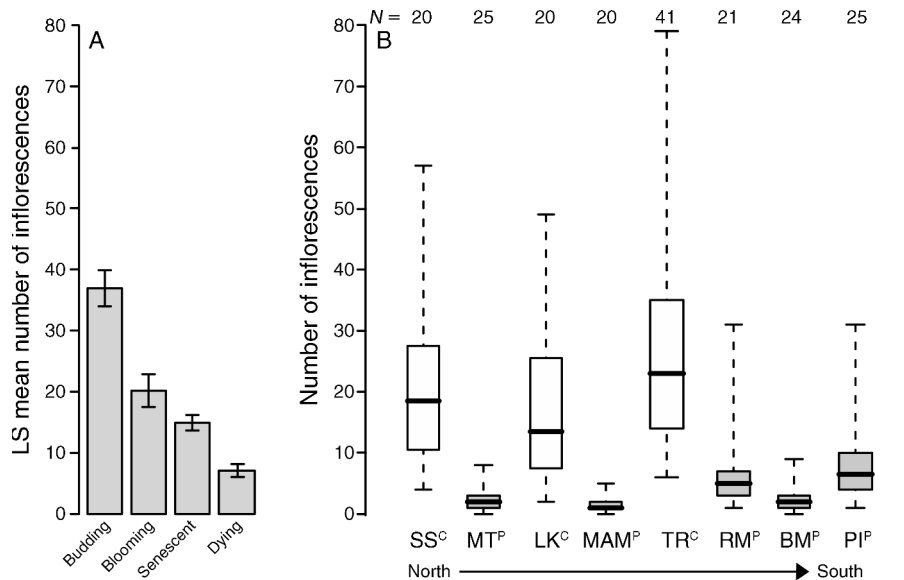
FIG. 4. Number of inflorescences on mature Ctor plants is associated with longevity and varies among sites in a way that predicts whether or not the host is used by local butterflies. (A) The y-axis shows the least-square mean number of inflorescences (buds + flowers + seed capsules) counted on plants that were budding, blooming, senescent, or dead within 30-cm quadrats at RM^P and TR^C. Variation among plants at the different stages was highly significant (ANOVA, $P < 0.0001$). Error bars show standard error of the mean. (B) Distribution of inflorescence number recorded from plants growing at all eight study sites. Open boxes are sites where Ctor was the host; gray boxes are sites where Psem was the host. Boxplots show data median (thick horizontal line), 25th and 75th percentiles (lower and upper extent of box), and range (dotted lines). See Fig. 1 for site abbreviations and superscript explanation.

Collinsia parviflora) in the eastern Sierra Nevada (Singer and Parmesan 1993). If spatial variation in plant acceptability to insects was similarly important in the current study, we would expect the identity of the preferred plant species to depend, at least in part, on the site of origin of the plants being tested. Instead, our results from a fully crossed design show that this identity depended only on the origin of the butterflies (Fig. 2). In contrast to our prior study, spatial variation in host acceptability made no detectable contribution to the association mosaic. Spatial variation in oviposition preference of the butterflies was the proximate cause.

Evolutionary cause of the geographic mosaic: natural selection caused by host longevity

In the "study system" section we described a trade-off between butterfly fecundity and offspring survival that generates phenological asynchrony between E. editha larvae and annual hosts, with consequent larval mortality from host senescence (Singer and Parmesan 2010). Phenological stress is an important feature of E. editha populations using ephemeral hosts, and the sites studied here where Ctor is used (LK^C, TR^C) are no exception (Table 1). This context prompted us to devise a simple phenological stress index for each site obtained by dividing the mean condition of plants by the mean condition of contemporaneous insects. Values of this index were consistently and significantly higher at sites where Ctor was not used (Fig. 3A, Table 4). Insects

attempting to host-shift to Ctor at Psem-using sites would therefore encounter a phenological barrier (cf. Boughton 1999). These data identify a source of spatially variable natural selection on insect diet that operated across all seven sites in the directions expected if it were to drive the geographic mosaic of species' association.

The differences among sites in phenological synchrony between E. editha and Ctor could be due to variation in the plants and/or the insects. We investigated this question directly at a pair of sites (RM^P, TR^C) where snowmelt and seed germination were by chance synchronous in 2009. Butterfly phenology was well synchronized between the sites, whether estimated from wing wear on adults or, later, from proportions of their offspring in each instar (Fig. 3B). In contrast, Ctor phenology was far from synchronous (Fig. 3B). This difference in Ctor phenology, and hence the difference in phenological synchrony between plants and insects, was due to a difference in life span of Ctor. By using the number of inflorescences on mature Ctor as a surrogate for its longevity (Fig. 4A), we can extend this finding to eight study sites. Across these sites, where Ctor plants had few reproductive structures at maturity, implying shorter life span, they were avoided by the butterflies (Fig. 4B), which had instead adopted alternate perennial host plants, principally Psem. This was true despite the fact that the local Ctor were available in full bloom when the butterflies were ovipositing.

We emphasize that it is Ctor longevity, and not reproductive potential, that previous work suggests should be critical for the insects. Small size of Ctor, as indicated by paucity of inflorescences, does not deprive the insects of food, since the density of these plants is high (Table 3), frequently reaching 50 plants per quadrat in quadrats of only 5 cm radius (Parmesan 2000).

A stable mosaic or a transitional phase?

Geographic patterns of species' interactions can represent stages in coevolutionary processes that are out of phase with each other across space (Brodie et al. 2002, Stenberg et al. 2008). In our case, variation among sites in Ctor resistance, measured here as life span, might represent snapshots in similar cycles of host resistance and parasite preference. We do not think so. Instead, we suspect that the short life span of Ctor at sites where the insects do not use it results principally from constraints on its growth emanating from edaphic factors rather than from evolution in response to insect attack. This suspicion was first aroused by observations of dramatic increases in Ctor size and life span in response to fertilization by fire (see *Discussion: Hindcasting an anthropogenic host shift*). It was subsequently strengthened by experiments in which we compared life spans of Ctor grown in soils taken from different sites (Appendix E). In summary, we believe that variation in Ctor longevity represents a relatively stable spatial template against which the species' association mosaic has evolved.

On the assumption that spatial patterns of Ctor phenology are stable, we can ask whether the current species' association mosaic is also a relatively stable feature or a temporary pattern representing a transition in evolution of the insect between different states of monophagy. Because the proximate driver of the mosaic is insect preference, long-term stability would require a stable selection mosaic acting on this trait; natural selection on insect preference should be stabilizing in populations with both diets. We have shown, by experimental manipulation of oviposition in the field, that selection on oviposition preference of *E. editha* was stabilizing at eight sites where the diet was not engaged in a bout of rapid evolution (Singer et al. 1994). This set of eight sites included two of our current sites, PI[P] and TR[C]. Fitness was higher on Psem than on Ctor at the Psem-feeding site and higher on Ctor than on Psem at the Ctor-feeding site. At the Psem-feeding site it was clear from field observations that the principal cause of larval mortality on Ctor was host senescence. The few larvae that found themselves on persistent Ctor survived very well, just as did Psem-adapted larvae from PI[P] and RM[P] when fed Ctor in captivity (Singer and McBride 2010). In contrast, insects at the Ctor-feeding site suffered no phenological stress when transferred to the long-lived perennial Psem, but laboratory experiments explained their low fitness on this host in the field by showing that >90% of them (from both sites TR[C] and

LK[C]) were incapable of developing on it (Singer and McBride 2010, cf. Rauscher 1982). We conclude that natural selection on the butterfly's diet has indeed been stabilizing at our study sites, though its source at Ctor-feeding sites was not the mirror image of the source at Psem-feeding sites. Within the set of host-adaptive traits that varied among our study populations, the crucial trait necessary for using Psem was physiological adaptation to this plant, while the crucial trait for successful feeding on Ctor was not a trait of the insects at all, but the phenology of their hosts.

Hindcasting an anthropogenic host shift

Temporal changes in species' interactions may take longer to document than even persistent investigators can endure. Extending time into the past can give us more power, but hindcasting known events that have already occurred is less intellectually satisfying than successfully predicting the unknown future, and can seem facile or disingenuous. Nonetheless, hindcasting can be useful whether or not it succeeds. When hindcasting is accurate, we gain confidence in forecasting. When hindcasting gives an incorrect or incomplete picture of the true past, it can illuminate differences between study systems or between past and present environments. In this spirit, we examine the extent to which the present study hindcasts eco-evolutionary dynamic consequences of anthropogenic intervention at Rabbit Meadow (RM[P]).

The landscape-scale mosaic in the current study was distributed across hundreds of kilometers, with local metapopulations classed as single sites among which current movement of insects can be assumed negligible (Harrison 1989). In the 1960s and 1970s a different, much smaller, mosaic was created among habitat patches within an 8 × 10 km metapopulation at site RM[P]. Logging and burning generated a series of clearings from which Psem was removed and longevity of Ctor was increased as soil nutrients from fire extended its life span. At a stroke, humans generated variation among habitat patches in phenology of Ctor, the principal variable responsible for the selection mosaic in the current landscape study.

The butterflies quickly colonized the "improved" Ctor in the clearing habitat type but retained their traditional diet of Psem in the undisturbed patches, creating a mosaic of insect–host association somewhat like a miniature version of the landscape mosaic. However, there were important differences between the two mosaics. First, in the landscape level mosaic both hosts were present and abundant at the principal study sites while in the metapopulation-level mosaic Psem was absent from the clearing patch type. Second, in the landscape mosaic butterflies using the two hosts differed in complex host-adaptive suites, including geotaxis and clutch size (Singer and McBride 2010), while in the metapopulation we observed only simple differentiation in oviposition preference (Singer 1983, Singer and

Thomas 1996). Third, the landscape study deals only with selection acting on insects within each of the two habitat categories, not between them. It does not ask whether insect fitness differed between sites where different hosts were used, nor does it need to ask this question in order to account for the observed association mosaic. In contrast, at the metapopulation level extensive movement of insects occurred among patches of different type, so any difference between patches in population growth rate and any phenotype-based bias in dispersal had the potential to influence evolutionary differentiation among patches and population dynamics in both patch types. In consequence, selection on insect host preference in the metapopulation took two forms: (1) selection acting among patches where different hosts were used, comprised of between-patch differences in fitness and (2) selection within patches, comprised of relative fitnesses of different preference phenotypes within each patch type. Only the second form has an analogue in the landscape-level study.

To what extent does the present landscape study hindcast patterns of selection generated in the disturbed metapopulation? First, consider selection among patches. In the landscape study all sites where Ctor was phenologically suitable contained insects adapted to it and monophagous on it, suggesting that natural selection had favored the use of Ctor at these sites despite the presence of Psem. On this basis we can tentatively hindcast that fitness on the novel host, the improved Ctor in the cleared patches, should have been higher than fitness on Psem in the undisturbed patches. We write "tentative" because the expectation of fitness on Ctor is reduced, to an unknown extent, by the existence of multiple behavioral adaptations to Psem, for example in geotaxis and clutch size (Singer and McBride 2010). Despite this caveat, the hindcast matches observation: the mean rate of population growth was faster on Ctor in logged clearings than on Psem in undisturbed patches, and densities of emerging adults were higher in clearings (Thomas et al. 1996, Boughton 1999). As hindcast, the anthropogenic habitat was more suitable for the insects than the traditional habitat.

Next, consider selection acting within patches. Psem-adapted insects in the clearings, with no choice of host, should have been selected to quickly accept Ctor while not necessarily preferring it. Butterflies in the unchanged patches should have been selected to prefer Psem over short-lived Ctor, as they did in the landscape study. So a selection mosaic should have been set up, with selection favoring acceptance of Ctor in clearings and opposing it in undisturbed patches. This was indeed the case (Moore 1989, Singer and Thomas 1996, Thomas et al. 1996).

Now that we have hindcast and described the patterns of anthropogenic selection acting within and among the two patch types, can we also hindcast the overall eco-evolutionary dynamics of the disturbed metapopulation? Yes and no. We can do so in one respect: there was rapid

response to selection within clearings. Insects developing on Ctor and emerging in the clearings became significantly more accepting of Ctor between 1984 and 1989 (Singer and Thomas 1996).

However, it turns out that our hindcasting ends there because multiple effects of dispersal proved to be influential in the anthropogenic mosaic. First, there was the expected effect of dispersal out of clearings, where population growth was high. This process strongly affected populations in undisturbed patches, where both larval density and acceptance of Ctor by ovipositing adults became significantly associated with isolation from clearings (Singer and Thomas 1996, Thomas et al. 1996, Boughton 1999, 2000). Insects in undisturbed patches near the clearings suffered both increased competition and maladaptive evolution because the increased tendency to accept short-lived Ctor was detrimental.

Less expected was the strong role assumed by nonrandom dispersal (Edelaar et al. 2008, Clobert et al. 2009) in the metapopulation mosaic. Butterflies typically practice hierarchical resource choice, first choosing habitat patches and then choosing hosts within those habitats (Friberg et al. 2008). However, their assessments of habitat quality, and their resulting tendencies to emigrate, are affected by encounters with preferred and less-preferred hosts (Thomas and Singer 1987, Hanski and Singer 2001). In this case, *E. editha* with different genotypes for host preference expressed those preferences by assorting themselves among habitat patches with different host composition. We documented these reciprocal preference-biased movements between a cleared and an undisturbed patch by preference-testing recaptured females, some of which had moved between patch types and some of which had stayed in the patch where they were first observed (Thomas and Singer 1987).

Nonrandom dispersal affected patch dynamics in several ways. Despite the rapid evolution of greater Ctor acceptance, in the early 1980s most insects emerging from Ctor in clearings still preferred Psem and were biased toward migrating back to the traditional host and habitat. This tendency to emigrate from clearings drove relationships between patch size and insect density. Insects that were attempting to emigrate were better able to escape from small patches than from large ones, so insect density increased strongly with patch size of Ctor in the disturbed metapopulation and small patches remained uncolonized. In contrast, the (nonsignificant) trend at TR^C, where butterflies were adapted to Ctor, was in the opposite direction, for higher densities in small patches, and there was no minimum patch size for colonization (Thomas and Singer 1998, Singer and Hanski 2004).

A second effect of biased movement was on differentiation of host preference between patches of different type (cf. Ravigné et al. 2009). Systematic differentiation in acceptance of Ctor evolved between adjacent cleared

and undisturbed patches. Experimental raising of offspring in common environment showed that the preference difference between a clearing and an adjacent undisturbed patch was heritable (Singer and Thomas 1996). This difference was in the direction expected from the selection mosaic. However, despite appearances, patch-specific selection was not the principal cause of this inter-patch difference in preference, because the difference persisted undiminished when the butterflies in the clearing were all immigrants, after a summer freeze had killed the hosts and starved all the larvae in the clearing (Singer and Thomas 1996). Our conclusion was that the preference differences between butterflies in cleared and undisturbed patches were not caused principally by selection, but were a manifestation of phenotype-biased migration that caused nonrandom gene flow and mimicked the effects of the selection mosaic.

In sum, the anthropogenic eco-evolutionary dynamics were more complex than expected from the successfully hindcast selection mosaic. The success of hindcasting reinforces the paramount importance of Ctor phenology to the insects. On the other hand, its incompleteness exposes the importance at metapopulation scale of gene flow, including biased dispersal, a phenomenon that was not detected as a generator of the landscape-level patterns. Traditional effects of gene flow drove maladaptive evolution of host preference in undisturbed patches, while biased dispersal drove relationships between patch size and insect density as well as differentiation between insects in adjacent patches of different type.

It is beyond the scope of this paper to hindcast the series of climate-related disasters in the 1990s that eventually drove the insects at Rabbit Meadow back to the ancestral condition of Psem-feeding that we found in our current study. However, the hindcasting that we do attempt, that of initial insect responses to anthropogenic changes of Ctor longevity, illustrates how both the selective and mechanistic underpinnings of geographic mosaics might be used to forecast anthropogenic effects on species' interactions. As we humans cause more and more large-scale environmental change, we expect such predictions of temporal change made from spatial pattern will acquire more and more practical value. For example, this approach should help predict how species distributions and partner affiliations will change in application of restoration techniques or in biological control.

Published evidence usually fails to record potential interactions

We searched for examples of species' association mosaics in the literature, but it was generally difficult to decipher how widespread they may be. There has been much interest in the use of resources as a function of their availability (Ivlev 1961, Winemiller and Pianka 1990) and in use of such data as measures of niche breadth or ecological specialization (reviewed by DeVictor et al.

2010). However, studies with this emphasis usually lack an explicit geographic component. There is also extensive documentation that focal species interact with different partners at different sites (e.g., Nylin 1988, Daltry et al. 1996, Travis 1996, MacLeod et al. 2001, Scriber 2002, LaJeunesse et al. 2004, Thompson 2005, Hoberg and Brooks 2008). However, in this type of study the relative abundances of actual and potential partners are often not mentioned, let alone measured, so it is usually not clear whether these examples constitute species-association mosaics. For example, Malaysian pit vipers switched between feeding principally on reptiles and on homeotherms (birds and mammals; Daltry et al. 1996). It seems highly likely that spatial variation in community composition was inadequate to explain this pattern, but Daltry et al. did not ask this question, perhaps because the answer was obvious to them as they worked in the field. Likewise, coral polyps switched their associations between different symbionts (LaJeunesse et al. 2004). Here the authors were explicit that they did not know the relative availabilities of the different symbionts at each site, so they could not tell to what extent community composition would account for the spatial variation in symbiont association. In sum, documentation of species-association mosaics by our definition has been rare, principally because researchers have, understandably, concentrated on interactions that did occur, at the expense of recording those that did not (exceptions include Singer and Parmesan 1993, Sword and Dopman 1999, Kuussaari et al. 2000, Kniskern and Rausher 2006).

Increasing study of spatial pattern beyond two-species systems

Strauss and Irwin (2004) and Agrawal et al. (2006) use wide-ranging reviews to argue that study of the evolution of plant–herbivore interactions should be informed by community ecology. Specifically, they state, such evolution cannot be understood by imagining communities to be assembled from interacting species pairs (cf. Muola et al. 2010). It is clear that genetic variation among individuals or populations can drive the community composition of species associating with them (e.g., Maddox and Root 1990, Johnson et al. 2009, Pantel et al. 2011). Agrawal et al. (2006) argue that insect host shifts should be studied in the light of plant community structure, despite the fact that "studies involving multiple interactors rapidly become cumbersome and difficult to manipulate." This raises the question as to what are the different levels of complexity that are appropriate and amenable to study (Bolnick et al. 2003, Forister et al. 2012). Here, we have developed an example involving just three species, an herbivore and two hosts. The switching of allegiance among partners that we document could not occur in communities assembled from fixed species pairs. By its very existence, it supports the arguments made by Strauss and Irwin and Agrawal et al.

Conclusion

We define "association mosaics" as deviations from a null expectation in which the extent or strength of ecological interaction between particular species varies spatially according to the availability of each species to the other. Our documented example is an extreme manifestation of such a mosaic, in which deviation from the null achieves its maximum possible value. We provide both a mechanistic and an evolutionary basis for this pattern. We attribute maintenance of the association mosaic to a selection mosaic acting on the insects as a result of differences in phenology of their annual host, Ctor. At sites where Ctor has small size and short life the butterflies have evolved to attack a different plant species, one that is longer-lived by virtue of its perennial life history and hemiparasitism of trees. This evolutionary cause contrasts sharply with the proximate cause of the mosaic, which reciprocal transplants identified as spatial variation in fixed, genetically based, butterfly oviposition preferences for the different host species, irrespective of plant size or phenology.

What might be the practical and conceptual uses of improving our knowledge of such patterns? It should help us to develop tools to predict future events at the community level, including the identities of species that will interact at particular times and places. It should also aid in testing hypotheses about landscape-level eco-evolutionary dynamics (Hoberg and Brooks 2008, Loeuille and Leibold 2008). We hope that our comments will stimulate attention to the complex causes of geographic mosaics in species' associations.

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SUPPLEMENTAL MATERIAL

Appendix A

Latitudes, longitudes, and elevations of study sites (*Ecological Archives* E093-247-A1).

Appendix B

Classification of phenological stress in Ctor-feeding sites (*Ecological Archives* E093-247-A2).

Appendix C

Consistency over time of host use at each site (sites listed from south to north) (*Ecological Archives* E093-247-A3).

Appendix D

Oviposition host preferences of butterflies caught in the field and tested on plants gathered either at their own site or at a different site (*Ecological Archives* E093-247-A4).

Appendix E

Longevities of Ctor transplanted as newly germinated seedlings into soils from sites where *E. editha* uses different hosts (*Ecological Archives* E093-247-A5).