Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly

Ilkka A. Hanski[1]

Department of Biosciences, University of Helsinki, FI-00014, Helsinki, Finland

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Demographic population dynamics, gene flow, and local adaptation may influence each other and lead to coupling of ecological and evolutionary dynamics, especially in species inhabiting fragmented heterogeneous environments. Here, I review long-term research on eco-evolutionary spatial dynamics in the Glanville fritillary butterfly inhabiting a large network of approximately 4,000 meadows in Finland. The metapopulation persists in a balance between frequent local extinctions and recolonizations. The genetic spatial structure as defined by neutral markers is much more coarse-grained than the demographic spatial structure determined by the fragmented habitat, yet small-scale spatial structure has important consequences for the dynamics. I discuss three examples of eco-evolutionary spatial dynamics. (*i*) Extinction-colonization metapopulation dynamics influence allele frequency changes in the phosphoglucose isomerase (*Pgi*) gene, which leads to strong associations between genetic variation in *Pgi* and dispersal, recolonization, and local population dynamics. (*ii*) Inbreeding in local populations increases their risk for extinction, whereas reciprocal effects between inbreeding, population size, and emigration represent likely eco-evolutionary feedbacks. (*iii*) Genetically determined female oviposition preference for two host plant species exhibits a cline paralleling a gradient in host plant relative abundances, and host plant preference of dispersing females in relation to the host plant composition of habitat patches influences immigration (gene flow) and recolonization (founder events). Eco-evolutionary spatial dynamics in heterogeneous environments may not lead to directional evolutionary changes unless the environment itself changes, but eco-evolutionary dynamics may contribute to the maintenance of genetic variation attributable to fluctuating selection in space and time.

habitat loss and fragmentation | life history ecology | population age

The idea that microevolutionary dynamics influence ecological population dynamics was clearly articulated in the 1950s by Dennis Chitty, a Canadian ecologist working with Charles Elton in Oxford, United Kingdom, at the time. According to Chitty's hypothesis (1), cyclical dynamics of temperate and arctic small mammals are maintained by high population density selecting for aggressive individuals, which are good competitors but have such a low rate of reproduction that the population declines when their frequency becomes high, after which selection starts to favor nonaggressive individuals with a high rate of reproduction, leading to the next cycle. Although the Chitty hypothesis was rejected by the 1990s, it exemplifies well the possibility of reciprocal eco-evolutionary dynamics, also called eco-evolutionary feedbacks (2), in which evolutionary dynamics influence ecological dynamics, and vice versa. In recent years, there has been a renewed interest in eco-evolutionary dynamics (3–5), and especially in the possibility that a population's genotypic or phenotypic composition influences ecological changes in populations (6–8), and even in communities and ecosystems (9, 10); a smaller number of studies have examined the reciprocal effects (e.g., 11–13). Even the unidirectional version of eco-evolutionary dynamics represents a new and important perspective to ecologists, challenging the long-held view of disparate time scales of ecological and evolutionary dynamics (14).

In theoretical population biology, there has been much interest in reciprocal eco-evolutionary dynamics for a long time. Models of source-sink dynamics (15), evolutionary dynamics of ecological niches (16), and the determination of species' range boundaries (17) involve feedbacks between local adaptation, gene flow, and demographic dynamics. As another specific example, Abrams and Matsuda (18) showed with a predator-prey model that the evolutionary dynamics of prey vulnerability may lead to a qualitative change in demographic predator-prey dynamics, a prediction that has been verified in chemostat experiments on algae and their rotifer predators (13).

Reciprocal eco-evolutionary dynamics are not equally likely to occur under all ecological circumstances. It has been argued that eco-evolutionary dynamics are most common during transient periods following environmental changes (19); on that basis, they could be expected to be especially prevalent in situations that are characterized by continuing changes. An example of such circumstances, and the one examined in this article, is metapopulation dynamics in heterogeneous environments with frequent local extinctions and establishment of new populations by dispersing individuals. Colonizations are likely to select for life history traits that are not selected for in established populations (20), generating spatial variation in the direction and strength of natural selection among populations with dissimilar demographic histories. Additionally, whenever there is spatial variation in habitat type, populations may become locally adapted; in such case, gene flow and founder events often involve individuals that are poorly adapted to the environmental conditions they encounter following dispersal, with likely consequences for the demographic and evolutionary dynamics of populations. The spatial scale and the magnitude of dispersal will influence local adaptation; however, equally, the degree of local adaptation may influence dispersal and local demographic dynamics.

In this article, I review research that has been conducted on the Glanville fritillary butterfly (*Melitaea cinxia*) in a highly fragmented heterogeneous environment in the Åland Islands in Finland for 20 y. I start by describing the environmental setting and the demographic and genetic spatial structures and dynamics of the metapopulation. We have discovered surprisingly strong associations between molecular variation in the phosphoglucose isomerase (*Pgi*) glycolytic gene and many life history traits and fitness components, which I review briefly, because these associations underpin the dynamics involving dispersal. The rest of the article describes three facets of eco-evolutionary spatial dynamics in the Glanville fritillary: extinction-colonization dynamics and the evolution of dispersal; inbreeding, mutational meltdown, and extinction; and the evolution of host plant preference, dispersal, and the establishment of new local populations. Throughout the article, I supplement the review with selected new analyses, which are identified as such in the text.

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[1]E-mail: ilkka.hanski@helsinki.fi.

Glanville Fritillary Metapopulation

The Glanville fritillary is a relative of American checkerspot butterflies and is widely distributed in Europe and temperate Asia (21). In the Åland Islands in Finland, it inhabits a large network of approximately 4,000 dry meadows with at least one of the two larval host species, *Plantago lanceolata* and *Veronica spicata* (Fig. 1*A*). The meadows are small, with an average area of 0.17 ha; only 3% are greater than 1 ha, and none is greater than 10 ha. The meadows occur within an area of 50 × 70 km on the main Åland Island and a few other large islands (Fig. 1*A*). The meadows differ from each other in terms of their area and host plant composition (Fig. 1*A*) as well as in many other respects (22).

Hanski (21) and Ehrlich and Hanski (23) have reviewed the life history of the Glanville fritillary [more specific studies on the adult life history include those by Saastamoinen (24) and Kuussaari et al. (25)]. I highlight here one particular feature that is important in the present context: females lay their eggs in large clutches of 150–200 eggs at intervals of a single day to several days depending on weather conditions, and the larvae live gregariously in groups of full sibs until the last larval instar in the following spring, having spent the winter in a silken "winter nest" spun by the larvae at the base of the host plant. Gregarious larval behavior has various biological consequences (26), but it also makes it possible to conduct large-scale surveys of the entire metapopulation by counting and sampling the conspicuous winter nests in early autumn (*Methods*).

Demographic Spatial Structure and Dynamics. Local populations inhabiting individual meadows are small. As an example, there were 727 local populations detected in the entire network in the autumn of 2004, of which 196 consisted of just a single larval group and only 136 had more than 10 larval groups; the very largest local population had 143 larval groups (detection probability is discussed in *Methods*). Larval groups have around 100 larvae in the autumn, but because the larvae in each group are mostly full sibs (27), the genetic effective sizes of the populations are small. Much mortality occurs at the larval stage, and the survival of larvae in the same group is correlated to a large extent (22), which amplifies stochastic changes in population sizes. The small local populations are prone to go extinct for many reasons (28). Of the 464 meadows that had a local population in 1993, only 5 have been continuously occupied until 2010 and they all have gone through small bottlenecks. On the other hand, local extinctions are compensated for by the establishment of new populations by dispersing butterflies, and the metapopulation has persisted in a balance between stochastic local extinctions and recolonizations (21). Fig. 2*A* shows that the size of the entire metapopulation has remained relatively stable over the past 20 y despite a high rate of population turnover (Fig. 2*B*). The number of annual extinction events increases, and the number of colonization events decreases, with an increasing fraction of meadows occupied (Fig. 2*C*), thereby promoting stability at the metapopulation level.

Genetic Spatial Structure and Dynamics. The genetic spatial structure of a metapopulation can be described by clustering local populations based on their allele frequencies in neutral markers (*Methods*). Fig. 1*B* gives the result based on four microsatellites and 10 SNPs. Comparing Fig. 1 *A* and *B* shows that the genetic spatial structure is much more coarse-grained than the demographic structure. Genetically homogeneous clusters typically include tens of discrete local populations as delimited by the physical structure of the environment. Genetic similarity is attributable to substantial gene flow among nearby populations. Both empirical (29) and modeling studies (11) indicate that roughly half of the butterflies in a population inhabiting an average-sized meadow disperse to at least one other meadow during their lifetime, up to a distance of 2–3 km from the natal population. A study of the genetic relatedness of the individuals that established new local populations in previously unoccupied habitat patches showed that the colonists, if more than one female was involved, typically originated from different source populations (30), which further increases the genetic similarity of nearby local populations.

One limitation of genetic studies based on a snapshot of data sampled in one generation is that the results are likely to reflect not only the spatial locations and the sizes of the local populations at the time of sampling, and the rate of concurrent gene flow between them, but the past demographic history of the metapopulation. Orsini et al. (31) found that the current genetic spatial structure of the Glanville fritillary metapopulation was better explained by the demographic spatial structure 5–7 y earlier than by the current demographic spatial structure, and current genetic diversity was significantly explained by past metapopulation sizes.

***Pgi* Polymorphism and Life History Traits.** The *Pgi* gene encodes for a glycolytic enzyme and is highly polymorphic in most species of animals and in many plants (32). Pioneering studies by Watt (33) demonstrated strong associations between PGI allozymes and individual performance and fitness components in natural populations of *Colias* butterflies. In the Glanville fritillary, Orsini et al. (34) identified a SNP in the coding region of *Pgi* (*Pgi_111*) as the key genetic variant at the DNA level (*Methods*). A series of studies has reported strong associations between *Pgi_111* and a range of life history traits (Table 1), with the AC heterozygotes typically exhibiting superior performance compared with the AA homozygotes (CC homozygotes are discussed in *Methods*). For

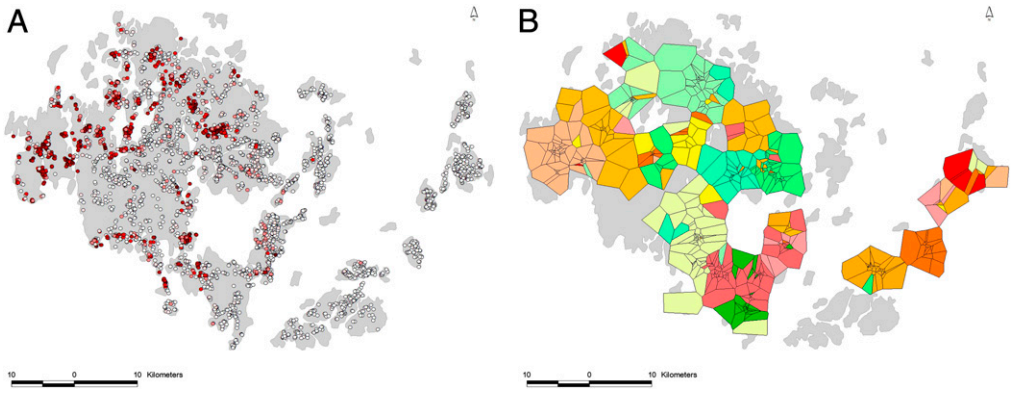

Fig. 1. (*A*) Map of the habitat patch network in the Åland Islands indicating the relative abundance of *V. spicata* in the meadows (darker color indicates greater relative abundance of *Veronica*; average values in 1993–2010). Gray shading shows land, and the rest is sea. (*B*) Genetic clustering of local populations based on four microsatellites and 10 SNPs (*Methods*). Clusters of local populations with homogeneous allele frequencies are indicated by different colors. Average genetic differentiation among the clusters was F_{st} = 0.05 (31).

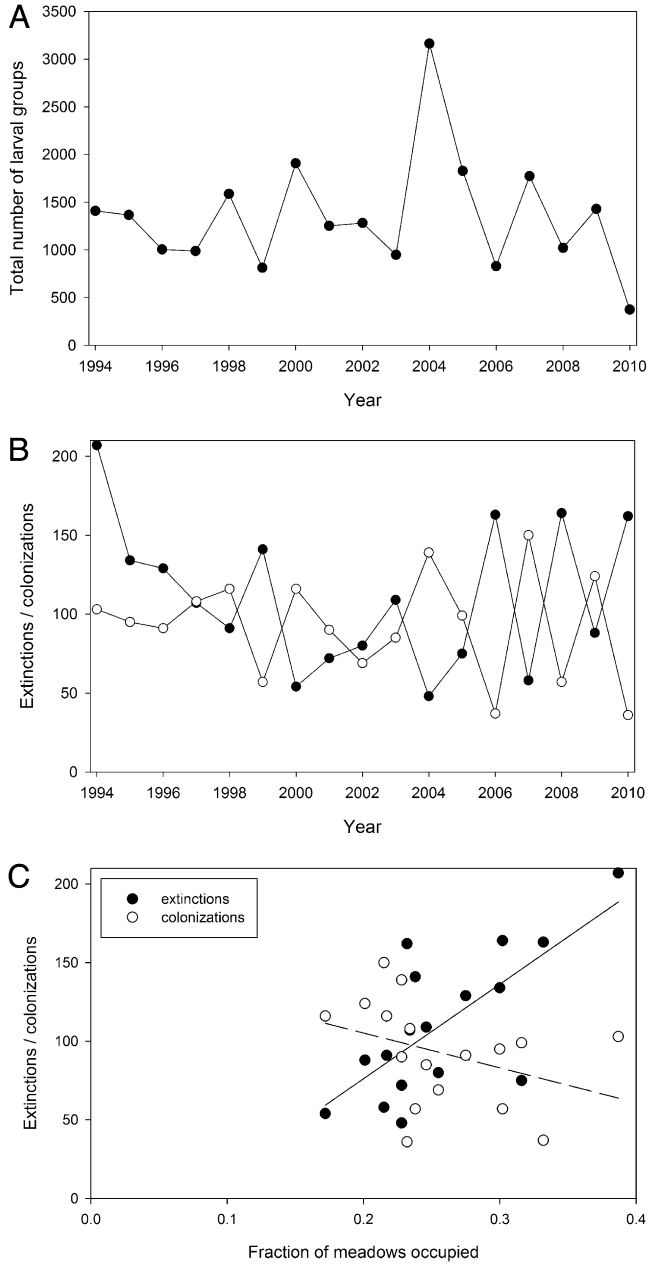

Fig. 2. Metapopulation size in terms of the total number of larval groups (*A*) and the numbers of local extinctions and recolonizations (*B*) per year in 1993–2010. The results were calculated for the meadows that have been surveyed every year in 1993–2010 (*Methods*). (*C*) Numbers of annual extinctions and recolonizations plotted against the fraction of meadows occupied in 1993–2010.

metapopulation dynamics, it is especially noteworthy that AC heterozygotes have roughly twice the flight metabolic rate (35) and fly roughly twice the distance in the field under commonly occurring low ambient temperatures compared with the AA homozygotes (36). Unfortunately, we do not yet have a causal understanding of these associations, and we cannot even be sure that *Pgi* is causally involved, although this seems very likely (34).

Eco-Evolutionary Dynamics

Colonization-Extinction Dynamics and the Evolution of Dispersal. Dispersal in heterogeneous environments influences ecological spatial dynamics as well as the dynamics of local adaptation via

Table 1. Effects of the *Pgi* genotype on life history traits in the Glanville fritillary

Trait	AC performance, %	Interactions with	Ref.
Flight metabolic rate	+50	Temperature, body size	35,36
Dispersal rate in the field	+70	Ambient air temperature	36
Body temperature at flight	+10	Ambient air temperature	79
Clutch size	+20	Complex interactions	25
Lifespan	+15	Reproduction, sex, resource availability	24,48
Pupal weight	−15	Temperature	80
Population growth rate	+ or −	Depending on population parameters	6

The second column indicates the difference in the performance of the AC heterozygotes in SNP *Pgi_111* in comparison to the performance of the AA homozygotes. The performances of the two genotypes are typically affected by other factors; hence, the figures given in the table are approximate and refer to commonly observed situations in the field or conditions used in laboratory experiments.

founder events and gene flow, and indirectly via life history tradeoffs involving dispersal (37). Furthermore, because dispersal itself has often been shown to evolve quickly, especially in colonizing species and in metapopulations in heterogeneous environments (38), dispersal in fragmented landscapes is a good candidate to exhibit reciprocal eco-evolutionary dynamics.

In metapopulations, individuals that have dispersed among local populations may represent a nonrandom set of individuals with respect to traits related to dispersal capacity; therefore, comparing dispersers and nondispersers might uncover variation that is significant for ecological and evolutionary dynamics. Making such a distinction among individuals is often difficult, but metapopulations with a high rate of population turnover offer a practical solution: Individuals in newly established populations are either dispersers or their offspring. In the case of the Glanville fritillary with around 1,500 documented recolonization events since 1993, it is easy to sample the offspring of females that established new populations and to compare them with individuals sampled from old populations. Although some of the latter are likely to be the offspring of dispersers, there is nonetheless a systematic difference between the two population types (*Methods*).

Three types of experiments have shown that female butterflies sampled as larvae from newly established populations are more dispersive than females sampled as larvae from old populations: mark-recapture studies of butterflies released at the same time in the same natural environment (39, 40), comparable tracking studies of free-flying butterflies by harmonic radar (41), and experiments on mobility in large outdoor population cages (25). Saastamoinen (42) has reported significant heritability of cage-measured mobility for females, supporting the assumption that the difference in mobility between new-population and old-population butterflies is genetically determined. Flight metabolic rate, measured as CO_2 output of butterflies encouraged to fly in a metabolic chamber, is higher in new-population than in old-population females (43, 44), and flight metabolic rate is positively correlated with dispersal rate in the field (36). There are also significant differences in other life history traits of females from new vs. old populations, but these differences do not support the commonly assumed tradeoff between dispersal capacity and fecundity (45–47). On the contrary, new-population females mature eggs at a faster rate (43) and initiate reproduction at a younger age than old-population females (25). New-population females may, however, do worse than old-population females when the availability of adult resources is low (48, 49).

At the level of genetic variation, new-population females have higher expression than old-population females of genes in the abdomen that are related to egg provisioning, which appear to be

regulated by higher juvenile hormone titer and angiotensin-converting enzyme mRNA (43). These results support the organismal-level results on faster egg maturation in new-population females. In the thorax, genes involved in the maintenance of flight muscle proteins exhibit higher expression in new-population females than in old-population females (43), apparently related to the higher flight metabolism in the former. Even more specifically related to dispersal, the SNP *Pgi_111* in the gene *Pgi* is highly significantly associated with flight metabolic rate (35) and dispersal rate in the field (36). Given these associations, one could expect that new populations are often established by individuals with the fast-dispersing *Pgi* genotype, the AC heterozygotes in *Pgi_111* (Table 1); hence, it is not surprising that the frequency of the AC heterozygotes is higher in newly established populations than in old populations (6). There is thus a pleasingly consistent pattern in the results concerning spatial variation of traits related to dispersal, all the way from the molecular to the physiological to the population level.

Zheng et al. (11) have constructed a detailed individual-based model of the dynamics of the metapopulation in the 4,000-patch network, parameterized with abundant empirical data. The model correctly predicted the higher frequency of the C allele (AC heterozygotes) than the A allele (AA homozygotes) in newly established populations than in old populations, and the model predicted that the frequency of the C allele increases with decreasing size of the patch network at the landscape level. This network-level prediction is strongly supported by the new empirical result in Fig. 3*A*, showing that among different subnetworks (50) of the entire 4,000-patch network, the frequency of the C allele decreases with increasing metapopulation capacity, a measure of the effective size of the network for the butterfly (*Methods*). Using the empirically based model, Zheng et al. (11) directly tested the influence of ecological changes (perturbation in population sizes) on evolutionary dynamics (*Pgi_111* allele frequency), and vice versa. Both effects were detected, but demographic changes had a stronger immediate effect on *Pgi* allele frequency changes than vice versa.

Inbreeding, Mutational Meltdown, and Extinction. Populations living in fragmented landscapes are threatened by multiple ecological and environmental factors, but their viability can also become compromised by inbreeding, random loss of beneficial mutations (leading to loss of adaptive potential), and random fixation of deleterious mutations (increasing genetic load) (51, 52). In the Glanville fritillary metapopulation, new populations are often established by just a single dispersing female (30), which means that matings among close relatives are common in the following generation. One generation of full sib mating leads to inbreeding depression (53, 54) that is substantial enough to increase the risk for local extinction (55, 56). Saccheri et al. (55) found that average heterozygosity as a measure of inbreeding accounted for 26% of total deviance in extinction risk among 42 populations.

Inbreeding depression decreases population growth rate, which tends to reduce population size. On the other hand, emigration rate is higher in smaller populations in the Glanville fritillary (57). Although elevated emigration from small populations may not be an adaptation, to avoid inbreeding, in this case, it will nonetheless have the effect of increasing gene flow between populations, and thereby decreases inbreeding. The reciprocal effects between inbreeding, population size, and emigration represent likely eco-evolutionary feedbacks.

Small populations and metapopulations may become purged of deleterious mutations to some extent, which would improve their fitness, or, conversely, deleterious mutations may become fixed by random drift and lead to gradual erosion of fitness. Finding out what actually happens in natural populations and metapopulations remains a largely empirical question. We have studied an informative example of an old, small, and completely isolated population of the Glanville fritillary on the small island of Pieni Tytärsaari (PT) in the middle of the Gulf of Finland in the Baltic Sea. The population was most likely accidentally introduced by humans before 1936. In autumn of 2009, the size of the population inhabiting the single meadow of approximately 10 ha was 111 larval family groups, corresponding to somewhat fewer than 100 reproducing females. Comparing butterflies from the Åland Islands, the fitness of the PT females was only 32% in terms of the number of prediapause larvae produced under common garden conditions in the laboratory. On the other hand, there was complete fitness recovery in crosses between the PT and Åland populations, suggesting a large genetic load in the former.

The metapopulation in the Åland Islands, with a census size of a few thousand individuals and a history of >100 y in isolation, does not experience reduced fitness in comparison to butterflies from the large island of Saaremaa in Estonia with large continuous populations. On the contrary, there is some indication of purging in the Åland metapopulation, because one generation of inbreeding reduced the egg hatching rate significantly less in this population than in a large continuous population from southern France (53). More research needs to be done on these questions, but these observations indicate both purging and rapid accumulation of genetic load depending on the size and spatial structure of populations.

Evolution of Host Plant Preference and Extinction-Colonization Dynamics. Checkerspot butterflies, like many other insect herbivores, use only one or a few larval host plant species in any one population, although there may be other plant species present that are used by conspecific populations at other localities (58). The Glanville fritillary is known to use nearly 10 species of *Plantago* and *Veronica* across its geographical range in Europe and Asia. In the Åland Islands, it has two host species, of which *P. lanceolata* occurs everywhere but *V. spicata* is restricted to the northwestern part of the study region (Fig. 1*A*). Genetically determined female host preference shows a matching cline, from

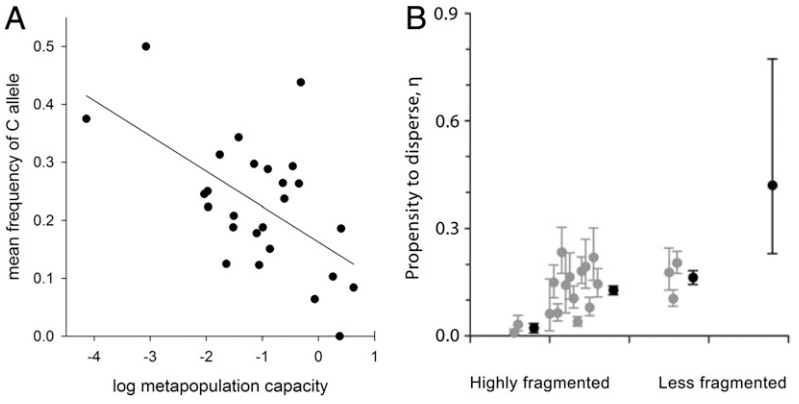

Fig. 3. (*A*) Dispersal rate in the Glanville fritillary as measured by the frequency of the C allele in the SNP *Pgi_111* in different subnetworks in the Åland Islands against the logarithm of the metapopulation capacity of the subnetwork (*Methods*). There is more habitat, and it is less fragmented, with increasing metapopulation capacity. The regression line is significant (P = 0.002, n = 26, R^2 = 0.30). (*B*) Dispersal propensity in the bog fritillary butterfly in mark-release-recapture experiments conducted in landscapes with different amounts of habitat (66). Gray symbols show yearly estimates with a 95% confidence interval, and black symbols show the estimates for pooled data for each of the four landscape types. Schtickzelle et al. (66) parameterized a model in which emigration rate from patch i is given by $\varepsilon_i = \eta A_i^{-\zeta_{em}}$; thus, dispersal propensity η gives the emigration rate from a meadow of unit area (1 ha).

preference for *P. lanceolata* in the regions where it is the only host species to preference for *V. spicata* where both species occur together (59). In addition, host plant use deviates locally from random use toward the use of the locally more abundant species, suggesting some degree of local or possibly regional adaptation (Fig. 4). Host plant use in a particular population is also influenced by host plant use in the neighboring populations (Fig. 4, legend), apparently reflecting the large-scale pattern.

Glanville fritillary females lay only up to six to eight egg clutches during their lifetime (25). It is hence not surprising that they should be choosy and spend much time in searching for the next host plant. During this search, a female may fly away from the small meadow and disperse elsewhere. Likewise, a female that has just arrived at a new meadow may not settle in and oviposit if the preferred host plant is absent or scarce. Such situations arise often in the field, because in addition to the geographical gradient in host plant relative abundances (Fig. 1*A*), there is more haphazard spatial variation in host plant composition at smaller spatial scales, reflecting differences in soil types and other environmental factors. In this situation, and assuming that populations are to some extent locally adapted in terms of host plant preference (Fig. 4), host plant preference may influence immigration. In support of this hypothesis, Hanski and Singer (60) demonstrated that the rate of colonization of currently unoccupied meadows is affected by the match between the deduced host preference of immigrants and the host plant composition of the target patch. In the absence of actual measurements of preference for hundreds of local populations, we used the observed host plant use in the populations around the focal habitat patch as a measure of the preference of the immigrants (*Methods*), which is a rough approximation but supported by the result in Fig. 4 and by the results of auxiliary experiments (60). I have now repeated this analysis with data for 18 y [Hanski and Singer (60) had data for 4 y], with the same result (Fig. 5). For instance, consider the annual probability of colonization of meadows that are surrounded by populations in which larvae use mostly *Veronica* and where, by assumption, females are *Veronica*-preferring. If the focal meadow has only *Plantago*, the annual colonization probability is roughly four times smaller, on average, than if the focal meadow has much *Veronica* (Fig. 5). The likely explanation is that dispersing females are more likely to settle in if the meadow has much of the preferred host plant. Note also the clear asymmetry in Fig. 5: Other things being equal, meadows with *Veronica* are more likely to become colonized than meadows with *Plantago* only.

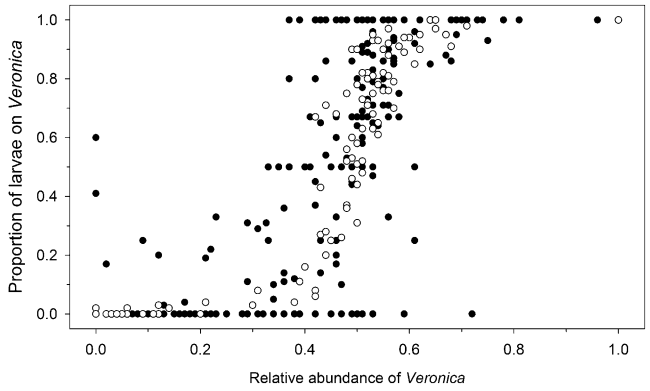

Fig. 4. Relationship between the proportion of larvae recorded on *Veronica* against the relative abundance of *Veronica* in individual local populations in the pooled data for 1993–2010. Open and solid dots indicate populations with ≥2 and <2 larval groups recorded per year on average. In a weighted logistic regression model for all 870 populations (weighted with the average number of larval groups), the effect of the relative abundance of *Veronica* was highly significant ($P < 0.0001$) and the relative use of *Veronica* in the neighboring populations ($R_{i,V}$; *Methods*) was also significant ($P = 0.0015$).

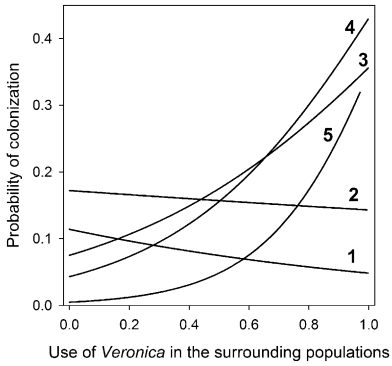

Fig. 5. Annual probability of recolonization of a currently unoccupied meadow in relation to the relative numbers of larval groups on *Veronica* in the surrounding populations ($R_{i,V}$; *Methods*). The latter measure is used as a proxy of *Veronica* preference among females immigrating to the focal habitat patch. The five lines are the fitted logistic regression lines to the data for habitat patches with different host plant species composition: 1, relative abundance of *Plantago* >0.9 (n = 5,841); 2, 0.9 > x > 0.55 (n = 780); 3, 0.55 > x > 0.45 (n = 1,256); 4, 0.45 > x > 0.1 (n = 599); and 5, <0.1 (n = 252). The results were calculated with data for the years 1993–2010.

Following the establishment of new local populations, their subsequent dynamics could be influenced by the match between the average preference of females and the local host plant species composition. Using the same approach as above for colonizations, I modeled the change in the sizes of local populations from year t to year $t + 1$ (*Methods*). I divided the meadows into those with only *Plantago* and those in which the relative abundance of *Veronica* was >50% (there are relatively few meadows with only *Veronica*; *Methods*). Additionally, I divided the populations into well-connected and isolated ones (*Methods*). The results show that, as expected, small populations tended to increase more than large ones; that populations inhabiting large habitat patches tended to increase more than the ones in small patches; and that populations tended to increase if many other populations in the same region increased (reflecting spatially correlated environmental stochasticity; Table 2). The effect of connectivity was positive in the generally well-connected populations but nonsignificant in isolated populations. This makes sense, because the low or very low level of immigration to the isolated populations is not expected to make a significant contribution to their demographic dynamics. Finally, the relative use of *Veronica* in the surrounding populations had a positive effect in *Veronica*-dominated populations and a negative effect in *Plantago*-dominated populations only if the population was well connected (Table 2). My interpretation of these results is as follows. In the well-connected populations, where immigration, as measured by connectivity, significantly increases population growth, the host plant preference of immigrant females influences their probability of settling in and reproducing, just as in the case of females arriving at unoccupied habitat patches, where they contribute to population establishment. In contrast, in the isolated populations, where immigration plays no significant role in the demographic dynamics, the host plant preference makes no significant difference, implying that host plant preference of resident butterflies, as reflected by host plant use in the surrounding populations, has no measurable effect on local dynamics.

Discussion

Ecological extinction-colonization dynamics and the evolutionary dynamics of local adaptation may commonly influence each other in species living in heterogeneous environments, of which the results on *Pgi* polymorphism in the Glanville fritillary is a clearcut example. Tracking studies of free-flying butterflies, allelic differences between newly established vs. old local populations, and other evidence indicate that the AC heterozygotes in the SNP

Table 2. Multiple regression models explaining the change in population sizes from year *t* to year *t* + 1 in local populations of the Glanville fritillary

	Plantago-dominated meadows				*Veronica*-dominated meadows			
	Well-connected		Isolated		Well-connected		Isolated	
Variable	Sign	*P*	Sign	*P*	Sign	*P*	Sign	*P*
Population size in year *t*	–	<0.0001	–	<0.0001	–	<0.0001	–	<0.0001
Area of the meadow	+	0.0001	+	0.0014	+	<0.0001	+	0.020
Connectivity	+	<0.0001	–	0.209	+	0.0047	+	0.019
Regional trend	+	0.0007	+	0.0001	+	<0.0001	+	0.0001
Veronica use, $R_{i,V}$ (*t*)	–	0.0016	–	0.890	+	0.025	+	0.408
R^2 (*n*)	0.30 (258)		0.23 (346)		0.43 (232)		0.30 (266)	

The material includes hundreds of local populations studied in the period 1993–2010 (*Methods*). The habitat patches have been divided into those dominated by *Veronica* vs. those dominated by *Plantago* and into well-connected vs. isolated populations. The explanatory variables are described in *Methods*. The signs in the table (+, –) indicate the direction of the effect. The last row gives the proportion of variance explained by the model with *n* in brackets.

Pgi_111 are superior dispersers to the AA homozygotes, and hence contribute disproportionately to colonizations. The genetic effect on colonizations is only a part of the story, however, because there are also other population dynamic consequences. Hanski and Saccheri (6) showed that the *Pgi* allelic composition of local populations influences their growth rate, which is not as surprising as it may first appear, because many life history traits, including fecundity and longevity, have been found to be associated with molecular variation in *Pgi* (Table 1). It is thus clear that the genetic composition of local populations affects the demographic dynamics.

One example of the reverse effect, the influence of ecology on evolutionary change, relates to the consequences of habitat loss and fragmentation on the evolution of dispersal, which has been much debated in the literature (61, 62). Two individual-based models constructed for the Glanville fritillary (11, 63) and the empirical data in Fig. 3*A* indicate that habitat loss and fragmentation select for increased dispersal in the Glanville fritillary by increasing extinction rate, and thereby the frequency of unoccupied habitat patches, which boosts the fitness of dispersers that may establish new local populations. A similar effect is found in invading species, in which selection favors a high dispersal rate at the current distribution border, where local populations have a ready supply of unoccupied patches just beyond the current border (64, 65). However, habitat loss does not necessarily increase dispersal rate, which is illustrated by the study of Schtickzelle et al. (66) on another butterfly species, the bog fritillary (*Proclossiana eunomia*). They conducted mark-release-recapture experiments in four kinds of landscapes and found that emigration rate was lowest in the most fragmented landscape (Fig. 3*B*). The essential difference between the two butterfly studies is the much greater stability of local populations in the bog fritillary. Thus, Baguette (67) reports that all habitat patches in small networks of 16–20 patches remained continuously occupied for 12 y, whereas similar small networks would not have viable metapopulations at all in the Glanville fritillary (68). The much greater stability of local populations in the bog fritillary is likely to be related to oviposition behavior: Whereas the Glanville fritillary lays eggs in large clutches of 150–200 eggs, the bog fritillary spreads the risks for offspring mortality by laying large numbers of very small clutches of 4–6 eggs. In the bog fritillary with relatively stable local populations, the dominant effect of habitat loss and fragmentation is a reduced rate of immigration attributable to generally smaller populations and elevated mortality during migration, which is expected to select against dispersal (69). This pair of butterfly species thus presents a nice example of how a difference in a life history trait (egg clutch size) may lead to a substantial difference in population stability, which influences the evolutionary response to changing landscape structure.

Turning to host plant preference by female Glanville fritillaries, we do not know which genes are involved, but the geographical cline in preference across the study area (59), paralleling a gradient in relative host abundances (Fig. 1*A*), strongly supports genetic determination. Singer et al. (70) have demonstrated significant heritability for host plant preference in Edith's checkerspot, a close relative of the Glanville fritillary. We have no experimental results on host preference for a large number of local populations, but the limited empirical evidence (Fig. 4) and modeling results (71) suggest that adaptation in terms of host preference has occurred largely at the network level rather than at the level of local populations. This is not surprising, because there is little time for strictly local adaptation to take place as a result of short lifetimes of local populations and because there is much gene flow among nearby populations, both increasing the spatial scale of adaptation in metapopulations (72). In contrast, in many populations of the Edith's checkerspot, which are larger and more isolated, there is more profound adaptation to different host plants, involving behavioral, physiological, and life history traits (73). McBride and Singer (74) have shown that hybrids between such locally adapted populations have greatly reduced fitness, which constitutes a powerful mechanism to reduce gene flow between populations that have become adapted to different host plants.

Thomas et al. (64) have described another butterfly example in which the evolution of host plant preference appears to have substantial consequences for spatial dynamics. The brown argus butterfly (*Aricia agestis*) in central England used to be restricted to warm habitats with the host plant *Helianthemum chamaecistus* (64). With a warming climate in the past 30 y, thermally less favorable sites have become suitable for the butterfly. These originally cooler sites have alternative host plants, *Geranium* and *Erodium* species, which are used in southern England but were not used previously in central England. Increasing thermal suitability of the cooler sites and the consequent improved performance of the respective local populations are expected to increase metapopulation size (Fig. 6) and have apparently allowed the species to expand in central England (64). However, a concurrent evolutionary change in host plant preference may lead to a shift from habitat and host plant specialization to network-level adaptation and to a much greater increase in metapopulation size (Fig. 6). The empirical results indicate that an evolutionary change in host plant preference has indeed taken place (64), which may have contributed to the observed increase in metapopulation size and range expansion.

In conclusion, results on dispersal, inbreeding, and host plant preference in the Glanville fritillary indicate significant reciprocal coupling between ecological and evolutionary dynamics. How widely can these results be generalized? I submit that there is nothing special about the Glanville fritillary; it exemplifies a large number of habitat-specialist species with a metapopulation

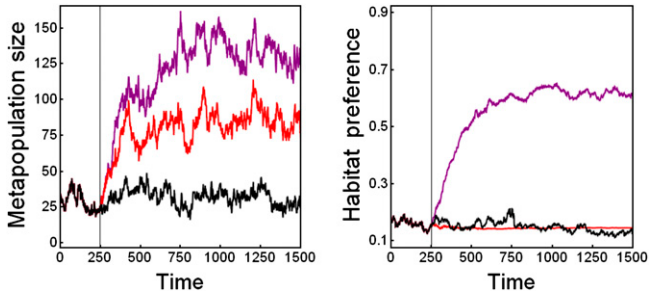

Fig. 6. Example of eco-evolutionary dynamics motivated by the study of Thomas et al. (64) on the brown argus butterfly and generated with the model of Hanski et al. (72). The example assumes a network of 400 habitat patches, of which two-thirds are initially of low quality [cool habitat, low population growth rate (r_0 = 0.4)], whereas the rest are of high quality (r_0 = 1.0). The black lines indicate metapopulation size (*Left*) and the mean value of habitat preference (*Right*, showing strong preference for the high-quality habitat). Following climate warming, the quality of the previously low-quality habitat improves (to r_0 = 0.95). In the absence of any evolutionary changes, the improved habitat quality increases metapopulation size, as indicated by the red line. In the presence of evolutionary change in habitat preference, the species evolves into a habitat generalist (violet line), for which the average phenotype across the network is given (*Right*), which further increases metapopulation size (*Left*). Parameter values (in addition to the ones mentioned above): v = 1, γ = 1, σ^2 = 0.01, δ = 0.8, c = 0.0003, and α = 1.0.

structure and fast extinction-colonization dynamics in heterogeneous environments. Insects and many other invertebrates have typically high intrinsic rates of population increase, which lead to fast demographic dynamics and potentially strong selection. Many such species have rather unstable local populations, for various reasons, which underscores the significance of dispersal, gene flow, and founder events in their spatial dynamics and may strengthen the eco-evolutionary feedbacks discussed in this article. Similar comments apply to species with expanding geographical ranges, in which dispersal and colonization are key processes, just like in metapopulations with a high rate of population turnover, although the range of the species is not moving anywhere in the latter case. The kind of eco-evolutionary spatial dynamics that I have discussed in this article may not often lead to directional evolutionary changes unless the environment itself changes, but eco-evolutionary dynamics may contribute to the maintenance of genetic variation attributable to fluctuating selection in space and time.

As a final remark, I point out the research opportunities that will emerge, in the near future, from combining the rapidly advancing genomic research on nonmodel species with the conceptual and theoretical framework of eco-evolutionary dynamics. The genomic research will greatly advance our understanding of the genetic basis of not only phenotypic and life history traits but of population dynamics. Conducting genomic research on natural populations in their heterogeneous environments will lead to new and stimulating questions about eco-evolutionary dynamics.

Methods

Survey of the Glanville Fritillary Metapopulation. The Glanville fritillary metapopulation in the Åland Islands in Finland has been surveyed since 1993. Initial mapping of the study region (50 × 70 km) in 1993 revealed a network of approximately 1,600 small meadows with at least one of the two host plant species present. The entire study region was remapped in 1998–2001, revealing a network of approximately 4,000 meadows, although the vast majority of the newly discovered meadows are very small and of low quality (22). In the present study, I included the set of meadows that have been surveyed every year from 1993–2010 to have entirely comparable data (Fig. 2).

A large number of field assistants search for and count the larval "winter nests" in late August to early September, when the silken webs spun by the larvae are most conspicuous (white) and the larvae have moulted to the diapause stage. We have estimated that the probability of detecting a web is around 0.5 (22). If no webs are found in a meadow, extra time is spent in searching to ascertain whether the meadow is really unoccupied. We have estimated that the probability of recording a meadow wrongly unoccupied is around 0.1 (22). The abundances of the host plants are scored on a scale from 0 to 3, separately for the two host plant species. On many occasions, we have sampled a small number of larvae from the larval groups for experiments and genetic analyses. In comparisons between newly established vs. old local populations, populations that did not exist in the previous autumn are classified as new populations, whereas old populations had existed continuously for at least 5 y.

For the analysis in Fig. 3*A*, the network of 4,000 meadows was subdivided into semi-independent subnetworks (50). I omitted networks with <20 meadows, and while calculating the network-wide frequency of the C allele in *Pgi_111*, I omitted local populations with fewer than four individuals genotyped. The smallest populations and networks were omitted because their allelic dynamics are much affected by genetic drift. Metapopulation capacity is a measure that captures the impact of network structure, the pooled area of habitat and its spatial configuration, on metapopulation persistence. Mathematically, metapopulation capacity is the leading eigenvalue of a matrix describing the network (75).

Host Plant Preference and Immigration. It is not feasible to measure experimentally the host plant preference of butterflies (76) in hundreds of local populations; hence, we have utilized host plant use as a rough measure of host preference [justified for the present purpose by Hanski and Singer (60)]. To analyze the effect of host plant use in the sources of migration on the rate of colonization of unoccupied meadows and on the annual change in population sizes, I calculated a measure of connectivity of a meadow/population i to larval groups on host plant V (*Veronica*; similarly for P, *Plantago*) in the surrounding populations as

$$S_{i,V}(t) = \sum_{j \neq i} N_{j,V}(t) e^{-\alpha d_{ij}},$$

where $N_{j,V}(t)$is the number of larval groups on host plant V in patch j in year t and d_{ij} is the distance in kilometers between patches i and j. The value of α was set to 1 based on the empirically observed average dispersal distance of 1 km (21). The rationale for this formula is that $S_{i,V}(t)$ is proportional to the numbers of potential immigrants to patch i that developed as larvae on *Veronica* (*Plantago*). Relative use of *Veronica* among the immigrants is measured by the ratio $R_{i,V}(t) = S_{i,V}(t)/(S_{i,V}(t) + S_{i,P}(t))$.

In the models in Table 2, the explanatory variables include the size of population i, measured by the logarithm of $N_{i,V}(t) + N_{i,P}(t) + 1$, and its connectivity, measured by the logarithm of $S_i(t) = S_{i,V}(t) + S_{i,P}(t)$. Spatially correlated changes in population sizes around the focal population were calculated as $T_i(t+1) = S_i(t+1)/S_i(t)$, which reflects the impact of spatially correlated environmental (weather) effects on population dynamics (77).

Genetic Spatial Structure. The genetic spatial structure of a metapopulation can be described by clustering local populations based on their allele frequencies in neutral markers. The purpose is to construct groups of local populations within which the allele frequencies are homogeneous but which are genetically differentiated from each other. The spatial genetic structure was described with data for four microsatellites and 10 SNPs (34) using the Bayesian analysis in the BAPS software (78).

***Pgi* Polymorphism in the Glanville Fritillary.** Large samples obtained from the Glanville fritillary metapopulation in 1995 and 2004 revealed seven allozyme alleles (44). Subsequently, we have identified three SNPs that map to three charge-changing amino acids in the coding region of *Pgi* (34). A combination of two of these SNPs corresponds to the allozyme allele *f* that was previously correlated with individual performance and fitness (6, 44). In practice, because of close linkage, the SNP *Pgi_111* alone explains phenotypic variation as well as the combination (34). In the Åland Islands, the two common genotypes are the AA homozygotes and the AC heterozygotes. The CC homozygotes occur much less frequently than expected in the Åland Islands, apparently because these individuals die at an early stage of development (34). The reason for the low fitness of CC homozygotes is not known, but the C allele may be linked to a recessive lethal mutation on a common haplotype. In many other parts of the geographical range of the Glanville fritillary, the CC homozygotes occur as frequently as expected.

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