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Interim Report **IR-03-028**

Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes

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Contents

Abstract

Species living in highly fragmented landscapes typically occur as metapopulations with frequent turnover of local populations. The turnover rate depends on population sizes and connectivities, but it may also depend on the phenotypic and genotypic composition of populations. The Glanville fritillary butterfly (*Melitaea cinxia*) in Finland uses two host plant species, which show variation in their relative abundances at two spatial scales: locally among individual habitat patches and regionally among networks of patches. Female butterflies in turn exhibit spatial variation in genetically-determined host plant preference within and among patch networks. Emigration, immigration and establishment of new populations have all been shown to be strongly influenced by the match between the host plant composition of otherwise suitable habitat patches and the host plant preference of migrating butterflies. The evolutionary consequences of such biased migration and colonization with respect to butterfly phenotypes might differ depending on spatial configuration and plant species composition of the patches in heterogeneous patch networks. Using a spatially realistic individual-based model we show that the model-predicted evolution of host plant preference due to biased migration explains a significant amount of the observed variation in host plant use among metapopulations living in dissimilar networks. This example illustrates how the ecological extinction-colonization dynamics may be linked with the evolutionary dynamics of life history traits in metapopulations.

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Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes

Ilkka Hanski
Mikko Heino

Introduction

Current interest in classic metapopulation dynamics is largely focused on questions about the persistence of species in highly fragmented landscapes (Settele *et al.,* 1996; McCullough, 1996; Hanski and Gilpin, 1997; Hanski, 1999, 2001). In empirical studies, the rates of population extinction and establishment are typically explained by ecological factors, such as the size and connectivity of local populations and the currently empty habitat patches (Hanski, 1998, 1999, 2001). Less attention has been given to the question to what extent population turnover might be influenced by the phenotypic or genotypic composition of local populations and the metapopulation as a whole. For instance, inbreeding depression can increase extinction rate of local populations (Saccheri *et al.*, 1998; Nieminen *et al.*, 2001), thereby potentially threatening metapopulation persistence (Richards, 2000), whereas local adaptations may diminish the risk of local extinction. These questions relate to the evolutionary dynamics of life history traits in metapopulations (Olivieri and Gouyon, 1997), including the process of classic group selection (Wynne-Edwards, 1962; Levins, 1970; Gilpin, 1975). With expanding ecological knowledge of species living in highly fragmented landcapes, it is both increasingly feasible as well as pertinent to merge questions about ecology and evolution in the metapopulation context. The most widely discussed trait in this context is migration rate, which indeed very clearly couples the ecological and evolutionary dynamics (Comins *et al.*, 1980; Olivieri and Gouyon, 1997; Travis *et al.*, 1999; Ronce *et al.*, 2000; Metz and Gyllenberg, 2001; Thomas *et al.*, 2001; Heino and Hanski, 2001). In this paper we consider the evolution of another life history trait in an insect species with a well-studied metapopulation structure in a highly fragmented landscape.

The large metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*) in the Åland Islands in SW Finland represents one of the best-studied classic metapopulations of any species (Hanski, 1999). A large number of ecological factors influence population turnover in this metapopulation (Hanski, 1998, 1999). Recently, Hanski and Singer (2001) reported a novel factor influencing the rate of population establishment in the Glanville fritillary, which uses two host plant species in the Åland Islands. They found that the probability of colonization of empty habitat patches is high when there is a good correspondence between the relative host plant species use in the surroundings of the focal patch and the host plant species availabilities in that patch. Hanski and

Singer (2001) tested all plausible hypotheses that could explain this ‘colonization effect’, and they concluded that it was caused by genetically-determined host plant preference of migrating females, which influences their movement behaviour and hence the chance of successfully colonizing empty patches.

In this paper, we address the evolutionary consequences of the colonization effect. We do this with a spatially realistic individual-based model, which attempts to predict the optimal host plant preference of butterflies living in a heterogeneous habitat patch network. The model is called ‘spatially realistic’ (Hanski, 2001) because the outcome of both ecological and evolutionary dynamics depend on the actual spatial configuration of the habitat patches in the network, including, in the present case, the host plant composition of individual patches. We start by summarizing the essential life history features and metapopulation structure of the Glanville fritillary in the Åland Islands. The magnitude of the colonization effect is illustrated, and we describe the mechanism leading to it, namely host plant preference-biased migration of female butterflies. These empirical results are then incorporated into a model of metapopulation dynamics to investigate the significance of the respective processes for the evolution of host plant preference. With the model, we infer the optimal host plant preference and host plant use in 24 distinct butterfly metapopulations. Finally, we test the model predictions by analysing whether they explain a significant amount of the observed variation in host plant use in these metapopulations. The answer to this question is affirmative, suggesting that host plant preference-biased movements and extinction-colonization dynamics influence the evolution of host plant preference in these metapopulations.

The Glanville Fritillary in the Åland Islands

In the Åland Islands in SW Finland, suitable habitat for the Glanville fritillary is represented by small dry meadows containing one or both of the larval host plant species, *Plantago lanceolata* and *Veronica spicata*. The mean, median and maximum patch areas are 0.13, 0.03 and 6.80 ha, respectively (*n*=1502; Hanski *et al.*, 1995). The habitat patches are located so far apart from each other that individual butterflies have no chance of sampling several patches in their lifetime (Hanski *et al.*, 1994, 2000; Kuussaari *et al.*, 1996). The large metapopulation of the Glanville fritillary in Åland represents a prime example of classical metapopulations, in which there are no large extinction-resistant local populations and which can hence persist only regionally in a balance between extinctions and colonizations (Hanski *et al.*, 1995; Hanski, 1999; Hanski and Ovaskainen, 2000).

The around 1,700 habitat patches that were known in the study area in 1993-97 have been divided into 127 patch networks, with little migration between the networks (Hanski *et al.*, 1996). We consider butterfly metapopulations in these networks to be dynamically independent. There are less than 127 such metapopulations, because many networks are empty at any particular time, typically because the network properties are not adequate for supporting a viable metapopulation (Hanski and Ovaskainen, 2000). Based on annual surveys of the habitat patches in 1993-97 (Kuussaari *et al.*, 2000; Hanski and Singer, 2001), we have the following data that are needed for the modelling described in this paper: spatial locations and areas of the habitat patches, the relative cover of *Veronica* (C_V), and the relative *Veronica* use by larvae in each habitat patch in 1993-97. The latter two variables have values in the range from 0 to 1. Additionally, for the purpose of illustrating the colonization effect, we use a measure of regional *Veronica* use in the neighbourhood of each habitat patch. To derive this measure, we first calculate for each patch i a measure of connectivity (Hanski, 1994) to larval groups on host plant X (*Veronica* or *Plantago*) in the surrounding populations in year t as

$$S_{i,x}(t) = \sum_{i \neq j} \exp(-\alpha d_{ij}) N_{j,x}(t), \tag{1}$$

where d_{ij} is the distance between patches i and j, $1/\alpha$ is the average migration distance, and $N_{j,X}(t)$ is the number of larval groups using host plant X in population j in year t. The value of α was set at 1 km^{-1} based on mark-release-recapture studies (Hanski *et al.*, 1994; Kuussaari *et al.*, 1996). A measure of regional *Veronica* use in the neighborhood of population i is then given by $R_i = S_{i,V} /(S_{i,V} + S_{i,P})$. This measure, which varies between 0 and 1, may be considered as giving the probability that a butterfly attempting oviposition in patch i fed as a larva on *Veronica*. .

Host Plant Preference-Biased Migration and the Colonization Effect

By the 'colonization effect' we refer to the influence of the regional host use R_i on the probability of an empty patch being colonized. Figure 1 illustrates the magnitude of the colonization effect as observed during four years of study (further analyses in Hanski and Singer, 2001). The graphs show the fitted logistic regression lines to data on observed colonization events as explained by the regional host plant use. It is evident that R_i explains a large amount of variation in the colonization rate.

In principle, the colonization effect could be caused by spatial variation in the quality of the host plants, by spatial variation in the quality of insects, or by both. Hanski and Singer (2001) examined the plausible mechanisms of the colonization effect in the Glanville fritillary. They reached the conclusion that it was caused by genetically-determined host plant preference of female butterflies. Thus a good correspondencethe a increases the rate of immigration to that patch and decreases the rate of immediate emigration, when there is a good correspondence between host plant preference of migrating butterflies and the host plant composition in that particular meadow (Hanski and Singer, 2001; Hanski *et al.*, 2002). The correspondence is relatively good on average, because female butterflies exhibit preference for *Veronica* in networks of high relative abundance of *Veronica,* where the use of *Veronica* is consequently also high (and *vice versa* for *Plantago*; Kuussaari *et al.*, 2000). 'Mismatches' occur in the case of habitat patches that have an atypical host plant species composition for the region, such as a *Plantago*-dominated patch in a network dominated by *Veronica*.

In conclusion, previous studies have conclusively demonstrated that host plant preference of migrating butterflies influences the rates of migration and colonization in heterogeneous patch networks. The question we address here is what are the evolutionary consequences of such biased migration and colonization rates.

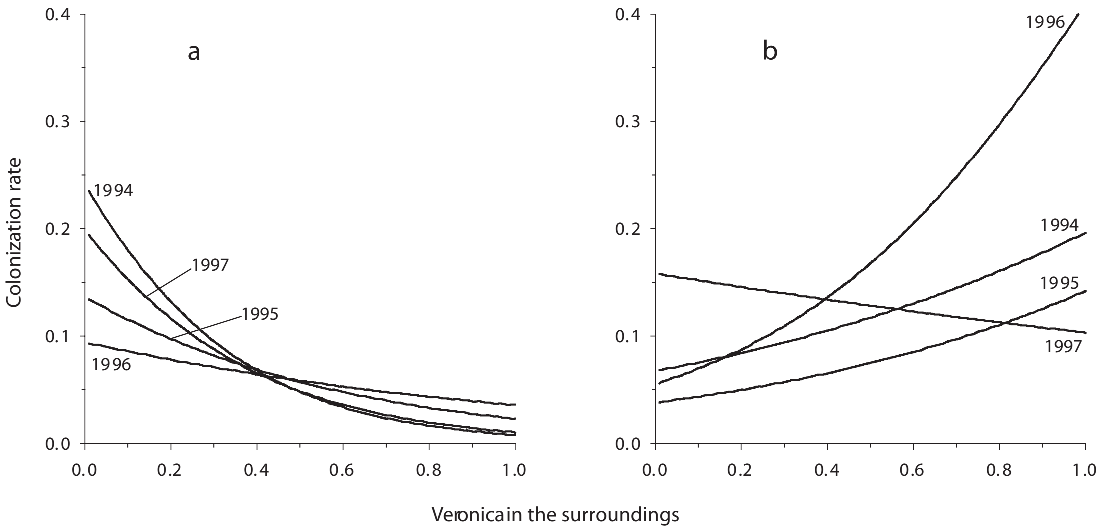

Figure 1: Illustration of the magnitude of the colonization effect described in the text and in Hanski and Singer (2001). Panel (a) shows the annual probability of colonization of *Plantago* dominated currently empty habitat patches as a function of *Veronica* use in the neighbourhood of the focal patch (R_i,Eq. 1). The figure shows the estimated logistic regression model for 4 years (1994-1997) for the average connectivity of the patches, which was also included in the logistic regression model (see Hanski and Singer, 2001). Number of patches in the four years was 346, 360, 370 and 432. Panel (b) shows the same results for *Veronica* dominated empty patches (n=89, 113, 101 and 92). For details see Hanski and Singer (2001).

Model

We employ a spatially realistic individual-based metapopulation model previously used to study the evolution of migration rate (Heino and Hanski, 2001). The model assumes a life history that closely corresponds with the life history of the Glanville fritillary and related checkerspot butterflies (Kuussaari, 1998; Hanski, 1999). We now extend the model to account for the effect of host plant preference on butterfly movements and oviposition behaviour. Specifically, we assume that host plant preference influences three aspects of behaviour. First, emigration probability is increased when a female prefers a locally uncommon host plant species. Second, immigration probability to a patch is correspondingly increased by high availability of the preferred host plant. Empirical results support these assumptions (Hanski *et al.*, 2002), which lead to the colonization effect illustrated in Fig. 1 (Hanski and Singer, 2001). Third, probability of ovipositing increases with increasing availability of the preferred host plant, which is a direct consequence of preference (Singer *et al.*, 1992). The Glanville fritillary lays eggs in clutches, maximally one clutch per day. We do not assume any effect of the host plant species on larval performance, for which there is no empirical evidence (van Nouhyus *et al.*, 2003). The latter result is actually surprising and raises the question about the cost of being a generalist. We do not know why females have specialized in the manner they have done in the Åland (Kuussaari *et al.,* 2000). One possibility is that a specialist is more efficient in locating a suitable host plant individual than a generalist (both host plants occur sparsely in the midst of other vegetation in the meadows).

The evolving primary trait in the model is host plant preference p_V, which varies from 0 (complete *Plantago* preference) to 1 (complete *Veronica* preference). The parameter p_V influences emigration, immigration and oviposition as explained above. We model the effect of preference on between-patch movements by modifying the migration model of Hanski *et al.* (2000), which is used here to describe the migration of adult butterflies in the evolutionary model (for a detailed description of the model see Heino and Hanski, 2001). The migration model assumes that daily emigration and immigration probabilities are power functions of patch area. We hence replace the real patch area with ‘perceived patch area’, which is a function of the host plant preference of the butterfly and host plant composition of the habitat patch. The perceived patch area is obtained by multiplying the real patch area by patch quality *q,* which is given by the following equation for a butterfly with preference p_V

$$q = p_V C_V^{\,*} + (1 - p_V)(1 - C_V^{\,*}). \tag{2}$$

Here C_V * is the perceived relative cover of *Veronica,* varying from 0 to 1. We assume that patch quality depends on the perceived relative cover of *Veronica* rather than on the actual cover, as it is unlikely that butterflies are able to accurately detect relative cover, especially when one of the two plant species is much less abundant than the other one. We used a scaled logistic function to describe C_V *, which allows for underestimation of the host plant species that is locally less abundant (Fig. 2). The dependence of patch quality on female’s preference and on the relative *Veronica* cover is illustrated in Fig. 2.

The perceived patch area A^* is now obtained as the product of the real patch area A and the patch quality q, $A^* = q\ A$. By replacing the real patch areas in the migration model of Hanski *et al.* (2000) by the perceived patch areas we obtain a model that includes the behavioural consequences of host plant preference: emigration probability is decreased and immigration probability is increased by a good match between host plant preference and host plant availability. With the exception that A is replaced by A^*, we follow exactly the use of the migration model of Hanski *et al.* (2000) as described by Heino and Hanski (2001). Parameter estimates were obtained from Hanski *et al.* (2000).

Host plant preference influences, by definition, oviposition probability (Singer *et al.*, 1992). We assume that oviposition probability increases linearly with patch quality,

$$P(\text{oviposit}) = 0.5\ q \tag{3}$$

We do not have data to support the linear relationship in quantitative terms, but Eq. (3) conforms qualitatively with the known behaviour of butterflies. The highest daily probability of laying an egg clutch is 0.5, which value takes into account that females do not lay at the maximal rate (one clutch per day) unless the environmental conditions are optimal (Heino and Hanski, 2001).

In order to have model predictions that can easily be compared with empirical observations we finally calculate the proportion of egg clutches laid on *Veronica* and *Plantago.* Note that this extra calculation does not play any functional role in the modelling of preference dynamics, this step is added only to predict by the model what can be observed empirically for each population. This submodel gives the probability

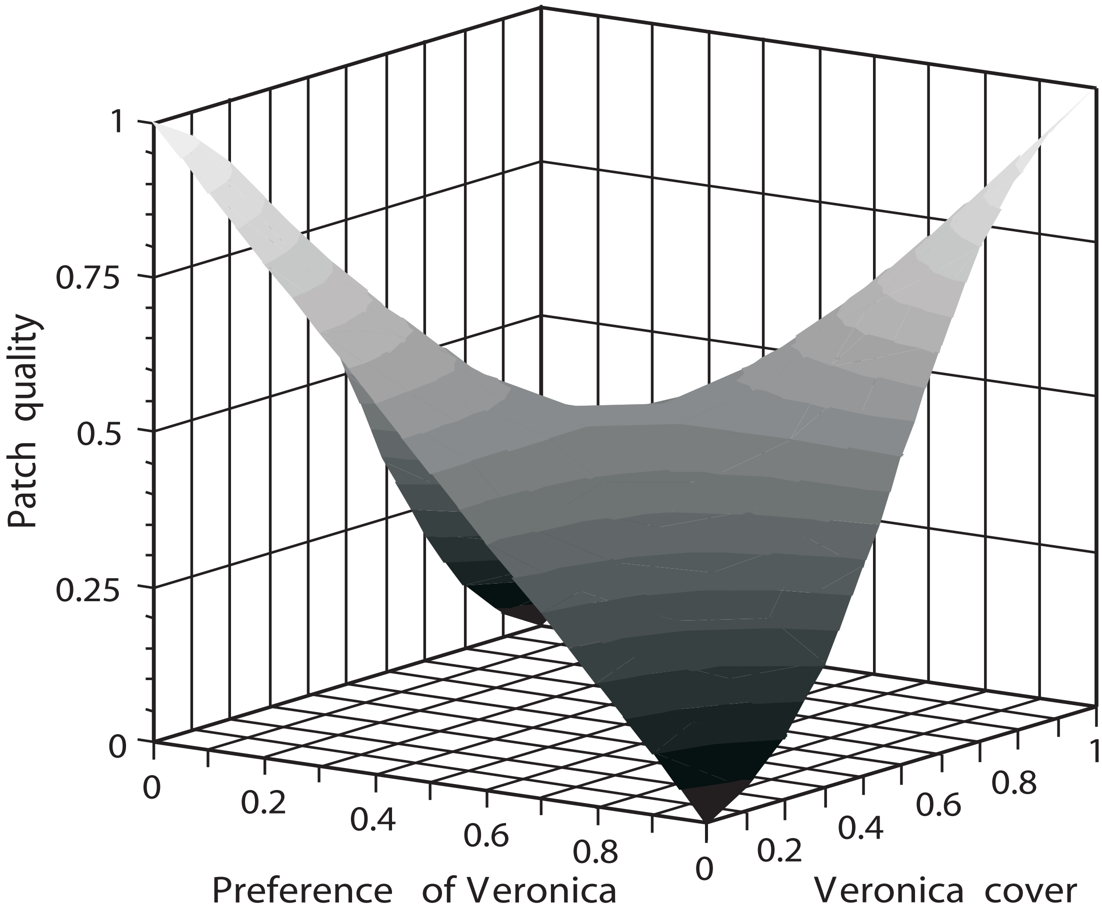

Figure 2. The dependence of the patch quality q on female's preference p_V and relative *Veronica* cover C_V. The highest perceived quality is achieved when a female shows complete preference for the host plant that has 100% relative cover. The surface was calculated with Eq. (1) and using the following formula to calculate the perceived relative cover of *Veronica*, $C_V^* = e^b(e^{2bC_V} - 1)/(e^b + e^{2bC_V})(e^b - 1)$. Parameter b is a shape parameter For b=1, the perceived cover is almost identical with the real cover. We used the value b=3 to generate this figure.

that an egg clutch is actually laid on *Veronica* once the female has "decided" to oviposit in the habitat patch (Eq. 3). We assume that host plant preference p_V equals the probability of accepting *Veronica* as the host plant once encountered. Similarly, 1-p_V equals the probability of accepting *Plantago* once encountered. If encounter rates with host plants are proportional to their relative abundances, the rate of encountering and laying on *Veronica* is proportional to $C_V\, p_V$ and on *Plantago* (1-C_V) (1-p_V). If the host plant is rejected, then the butterfly continues searching and encounters new plant individuals until one is accepted. If the search time is not a limiting factor, the probability of laying on *Veronica* becomes

$$P(\text{laying on } Veronica) = C_V p_V / (1 - C_V - p_V + 2C_V p_V). \tag{4}$$

Note that a butterfly with complete preference will never land in a habitat patch completely devoid of the preferred host plant (because in this case $A^* = 0$), which eliminates the potentially anomalous prediction of the above equation when there is a complete mismatch between preference and host plant availability ($p_V=1$ and $C_V=0$ or *vice versa*).

As a null model with no influence of preference on movement and oviposition behaviour, we used a model version with $q=1$ and $p_V = 0.5$. This model assumes that ovipositions on the two plant species occurs in proportion to their relative cover in the habitat patch in which the butterfly happens to be located.

Modelling Evolutionary Dynamics

We assume that both host plant preference (p_V) and emigration propensity (η) are evolving traits. The latter is defined in the migration model of Hanski *et al.* (2000) by an equation giving the daily probability of emigration from a patch with perceived area A^*,

$$\varepsilon = \eta A^{*-\zeta_{em}}$$

(see Hanski *et al.*, 2000; Heino and Hanski, 2001). Although we are primarily interested in the evolution of preference p_V, changes in preference influence movement behaviour and therefore evolution of host plant preference may influence optimal emigration propensity η. Hence we let the two traits coevolve simultaneously. The scaling parameter ζ_{em} is fixed at its empirically estimated value (Hanski *et al.*, 2000).

We assume that p_V and η are quantitative traits that are determined by many independent loci with small additive effects. Specifically, we assume 32 loci coding for one trait, each locus with two possible allelic states, ‘0’ and ‘1’. Mutations that flip the allelic state occur with a constant probability 0.001 independently in each locus. We assume that the two traits are not genetically linked and that inheritance is clonal. This latter assumption is not a drastic simplification because checkerspot females mate only once and typically in the patch in which they were born. Thus, relatedness of the offspring to the mother is likely to be high also in reality.

The genotypic value of a trait is determined by the number of ‘1’ alleles coding for it. The mappings from the genotype to the phenotypic value of the evolving trait are given in Fig. 3. The mappings were chosen in such a manner that the possible phenotypic values cover the feasible range of trait values, 0…0.25 for migration propensity (Heino and Hanski, 2001) and 0…1 for host plant preference. A problem with the chosen genetic architecture is that mutation distribution becomes strongly skewed for extreme genotypic values. This skew can counteract weak selection and prevent evolution to the phenotypic extremes. This was not a problem for migration propensity, for which phenotypes outside the range η=0.08…0.13 seldom persisted (Heino and Hanski, 2001). In contrast, extreme phenotypes are a likely outcome of evolution of host plant preference, and the skew becomes a potential problem. To overcome this problem, we truncated the mapping for preference in such a manner that the phenotypic extremes are achieved before the mutation distribution becomes strongly skewed (Fig. 3). This assumption allows evolution towards strong preference even when the selection pressure is weak.

Simulations were initiated with no preference ($p_V=0.5$) and optimal migration propensity obtained by running the model in the focal patch network without the effect

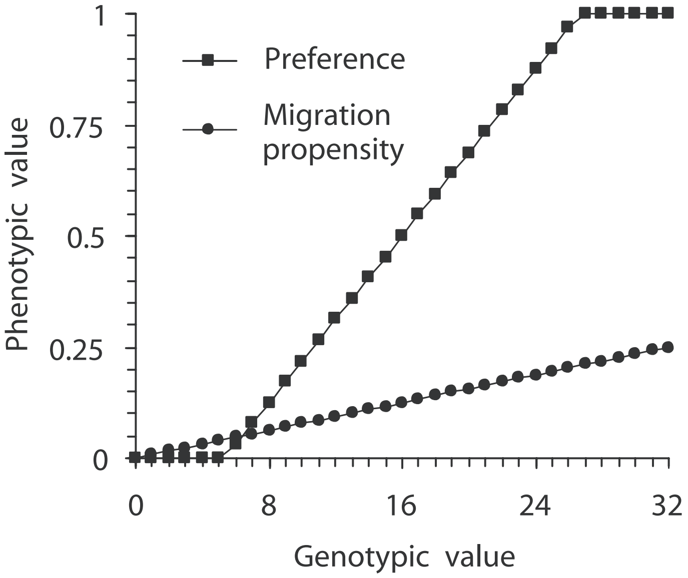

Figure 3. The mapping from genotypic to phenotypic values for the evolving traits in the model. The genotypic value of a trait is given by the number of ‘1’ alleles in the loci coding for the trait (details in the text).

of host plant preference (as in Heino and Hanski, 2001). Simulations were run for 1500 generations of which the first 500 were omitted as a transient. Predicted trait values were calculated as averages across individuals in the metapopulation. Eight replicate simulations were used to calculate the final results.

Results

The model was run separately for each patch network in which both host plants occur to find out the optimal value of host plant preference $p_{V.}$ Results could be obtained for those 24 patch networks in which the metapopulation persisted with high probability during the course of the simulation. The remaining networks are mostly so small that metapopulation extinction is likely to happen in a long stochastic simulation.

Figure 4 shows the observed *Veronica* use by larvae in the 24 networks plotted against the *Veronica* cover in the network as a whole, calculated as area-weighted average of the patch-specific relative covers C_V. There are three features in this relationship that should be noted. First, there is a tight positive relationship between the observed use of *Veronica* in a network and the respective *Veronica* cover (r=0.920, p<0.001). This relationship is of course expected even if there were no preference for either of the host plant species, in which case host plant use would simply reflect host plant availability. Second, the relationship is sigmoid, as previously analysed (Kuussaari *et al.*, 2000), indicating that there is disproportionate use of the more frequent host plant species in the network. Third, there is substantial variation around the overall trend, which is the critical information for the present study. This variation could reflect mere measurement errors in the empirically estimated variables, but similar trend and scatter as observed in the empirical data are also observed in the model-predicted results where measurement error is absent (Fig. 5). The modelling results are influenced by process

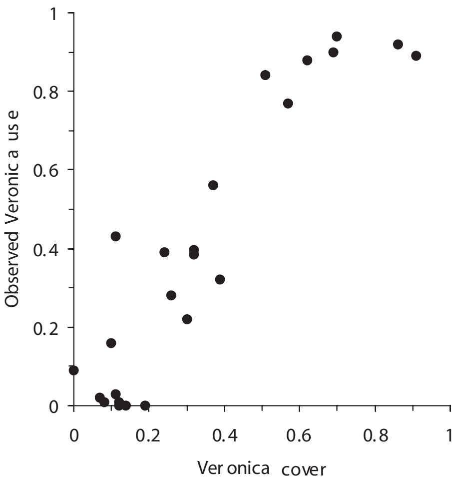

Figure 4. Fraction of larval groups found on *Veronica* in 24 patch networks against the relative cover of *Veronica* in the pooled data for 1993-97

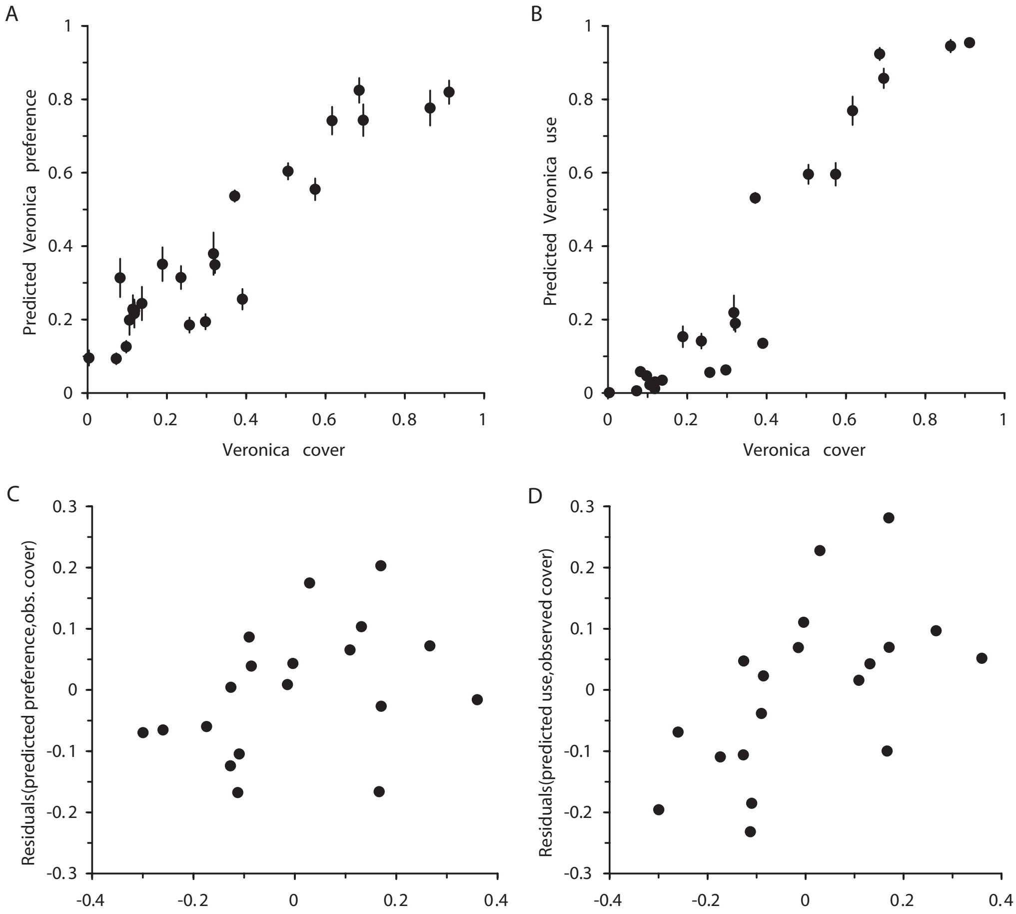

Figure. 5. Model predictions with 95% confidence intervals. (a) The predicted preference for Veronica and (b) the predicted proportion of egg clutches laid on Veronica against the relative Veronica cover in the 24 networks. The lower panels show residuals from regressions between observed Veronica use versus observed Veronica cover (Fig. 4) plotted against residuals from predicted Veronica preference (c) and Veronica use (d) versus observed Veronica cover. Residuals were calculated from linear regression with angular transformation to eliminate non-linearity (see Table 1) and are based on those 19 metapopulations where the host plant use of at least 10 larval groups has been recorded

Table 1. Regression models explaining the observed *Veronica* use in 24 metapopulations of the Glanville fritillary by *Veronica* cover in the network and by model-predicted *Veronica* use. The last two columns give partial correlation coefficients of model-predicted *Veronica* use with observed *Veronica* use when the effect of *Veronica* cover has been removed. Partial correlation analysis is restricted to those 19 metapopulations where the host plant use of at least 10 larval groups had been recorded.

Explained by	% of variance explained	partial correlation	
	R^2	r	p
Veronica cover	79.5		
Model without preference	87.4	0.534	0.022
Model with preference	89.8	0.592	0.010

Notes: In the regression models, networks were weighted with the number of larval groups observed in the network, to give more weight to networks with a large sample size. Angular transformation has been applied to all data in order to eliminate non-linearity and increase normality of residuals. The last two columns give partial correlation coefficients of model-predicted Veronica use with observed Veronica use when the effect of Veronica cover has been removed. Partial correlation analysis is restricted to those 19 metapopulations where the host plant use of at least 10 larval groups had been recorded.

error (variability due to demographic and environmental stochasticity), but such error was rendered small by running replicate simulations. We can hence expect that variability in the model-predicted results is mostly caused by metapopulation-level adaptation to the specific spatial configuration of the particular network, including the spatial distribution of the host plants in the patches. The key question is whether the variability observed both in the empirical data and in the modelling results reflects a common cause, which could only be metapopulation-level adaptation. We approach this question in two ways, by using regression models to explain the observed *Veronica* use and by analysis of covariation of the residuals, where the influence of *Veronica* cover on *Veronica* use has been removed.

We constructed regression models explaining the use of *Veronica* in each network either by the respective *Veronica* cover or by the model-predicted *Veronica* use. Among the 24 networks, *Veronica* cover alone explains almost 80% of variation in *Veronica* use (Table 1). There is thus not much variation left to be explained by the evolutionary model. Nonetheless, the model-predicted *Veronica* use explains the observations substantially better than *Veronica* cover (Table 1). The null model without the influence of preference on movements and oviposition however explains the observed *Veronica* use almost as well as the model in which the evolution of preference is included (Table 1). The fact that the null model predicts the observations better than *Veronica* cover in the network implies that the dynamics of the metapopulation in a heterogeneous patch network play a significant role in determining the observed pattern of host plant use.

We next calculated partial correlation coefficients between the empirically observed and model-predicted *Veronica* use, controlling for the influence of *Veronica* cover. This analysis corresponds to examining the correlation between the residuals in the plots in Figs. 4 and 5b. The residuals are positively correlated (Fig. 5c,d). The model-predicted *Veronica* use correlates significantly with the observed use both in the null model and in the model in which the influence of preference is included (Table 1). the were to 8dthe rate without the simultaneous evolution of host plant preference.

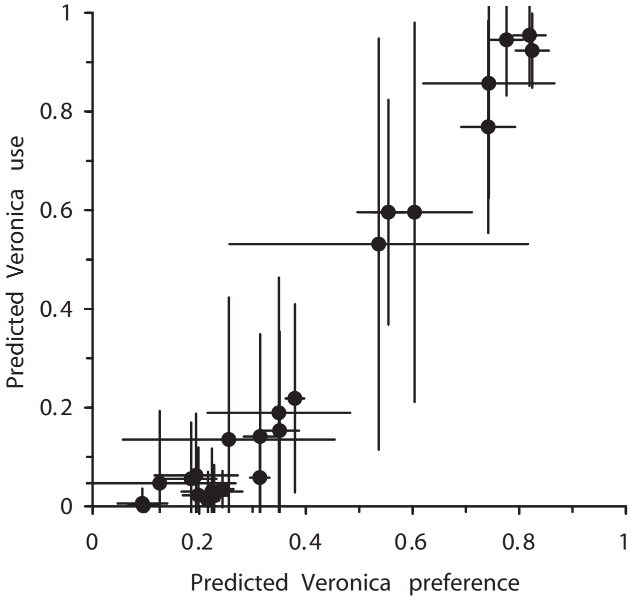

Figure 6. Variability of predicted *Veronica* preference and use within networks. Horizontal bars illustrate phenotypic variability in *Veronica* preference as measured by within network standard deviation in individual preferences. Vertical bars show the standard deviation of relative *Veronica* use among patches. This variability stems both from variation in *Veronica* preference among indivuals and from among-patch variation in relative *Veronica* cover.

Discussion

The model-predicted use of *Veronica* by the larvae of the Glanville fritillary butterfly in 24 habitat patch networks closely resembles the observed use of *Veronica.* First, the model predicts metapopulation-wide adaptation to the average conditions in the patch network: the predicted *Veronica* preference increases with relative *Veronica* abundance in the network as a whole (Fig. 5a). This prediction agrees with the observed patterns in *Veronica* preference (Kuussaari *et al.*, 2000) and *Veronica* use (Fig. 4). These results are not unexpected given the model assumptions, but they demonstrate that our evolutionary model behaves in a realistic manner.

Second, the model predicts substantial variation around the overall trend of increasing *Veronica* preference with *Veronica* abundance, which variation is caused by the spatial configuration of each patch network, including the manner in which the total amount of the two host plant species is distributed among the habitat patches. There are two distinct processes that operate at the level of patch networks and influence host plant use. First, the geometry of the network and the dissimilar roles of different patches in metapopulation dynamics cause butterflies to encounter the two host plant species non-randomly. Thus a habitat patch that is large and well-connected to other patches in the network has a higher incidence of occupancy by the butterfly than a marginal patch (Hanski and Ovaskainen, 2000), and hence plants in the former patch are more frequently encountered, and used, than plants in the latter patch. For this reason alone, the host plant use in a metapopulation can only partially be predicted with knowledge of network-wide host availability. Second, the model incorporating host plant preference and evolution of it predicts the observed host plant use slightly better than the model without preference, suggesting that host plant use may be influenced by metapopulation-specific adaptation. The model includes the selection operating in the metapopulations via preference-biased migration, which is manifested in the empirically-observed colonization effect illustrated in Fig. 1 (see section 'Host plant preference-biased migration and the colonization effect' in this paper; Hanski and Singer, 2001). Unfortunately, there is little variation in host plant use that remains unexplained when the influence of metapopulation dynamics is accounted for (the null model without preference), hence the opportunity to convincingly demonstrate metapopulation-specific adaptation via this approach is limited in this case. But given the conclusive empirical evidence for biased migration in the form of the colonization effect (Fig. 1), it would actually be surprising that there would be no evolutionary consequences of it.

Although the population-level colonization effect (Fig. 1) is clearly generated by individual behaviour, we may also interpret the biased colonization rate in terms of group selection playing a role in the evolution of host plant preference in these metapopulations. This interpretation stems from the observation that the preference p_V selected locally (in a particular habitat patch) is not the same preference which is selected by differential migration and colonizations at the metapopulation level. In our model, local selection favours the genotype that is completely specialized on the locally more frequent host plant, whereas selection at the metapopulation level selects for genotypes with intermediate level of preference (note the narrow confidence limits on model-predicted preference in Fig. 5a). Evolutionary biologists have debated the role of natural selection acting among populations for more than 30 years (Wilson, 1983; Williams, 1992; Harrison and Hastings, 1996; Goodnight and Stevens, 1997; Futuyma, 1997; Sober and Wilson, 1998). Opponents have argued that among-population or group selection must necessarily be weaker than within-population selection among individuals, because populations turn over at a much slower rate than do individuals within populations (Williams, 1966; Harrison and Hastings, 1996). Proponents point to the effectiveness of artificially applied group selection in laboratory experiments (Wade, 1976, 1978; Craig, 1982; Goodnight and Stevens, 1997). In this perspective, it would not be surprising to find that group selection occurs in the Glanville fritillary metapopulations in the Åland Islands, because the high turnover rate of local populations presents ample opportunities for selection to operate. Classical group selection is typically depicted in terms of differential population extinction (Wynne-Edwards, 1962; Levins, 1970; Gilpin, 1975), whereas in our case selection operates via differential population establishment. As a matter of fact, Hanski and Singer (2001) did not find host plant preference-biased extinction of local populations, comparable to the colonization effect shown in Fig. 1. Hanski and Singer (2001) discuss the biological reasons why host plant preference might not influence extinctions in these butterflies.

The influence of gene flow on local adaptation is well-established (e.g. Dias and Blondel, 1996), including cases where gene flow has influenced butterfly oviposition preference (Singer and Thomas, 1996). In the present case, the strong and consistent effect of host plant preference on the colonization of empty habitat patches with dissimilar plant species composition (Fig. 1; Hanski and Singer, 2001) implies the reverse effect: that metapopulation-level adaptation (of host plant preference) influences gene flow among populations. Because of the ephemeral nature of the local populations, butterflies have adapted to the conditions at the network level, in a manner that averages across local populations based on their role in the dynamics of the metapopulation as a whole. In this case, there is a potential coupling between the ecological extinction-colonization dynamics and the evolutionary dynamics of the life history trait of host plant preference. Evolution of migration rate in metapopulations provides another example of coupling between ecological and evolutionary dynamics (Olivieri and Goyun, 1997; Travis *et al.*, 1999; Thomas *et al.*, 2001; Heino and Hanski, 2001).

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