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Ilkka Hanski: The legacy of a multifaceted ecologist

Fugitive coexistence mediated by evolutionary lag in local adaptation in metapopulations

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Extinction–recolonization dynamics is known to promote "fugitive coexistence" in patchy environments: a species that is an inferior competitor but a better colonizer may persist by exploiting the period between its colonization of a patch and the arrival of a superior competitor. Here I use a simple model to demonstrate the plausibility of a different type of fugitive coexistence. I show that, under some circumstances, a "jack of all trades" plastic species can persist despite competition from an adaptable species that has the genetic potential to adapt locally and outcompete the plastic species in every patch. This persistence can be mediated by two forces that impede local adaptation: gene flow and extinction–recolonization dynamics. In the latter case, the persistence of the plastic species is of a fugitive nature; however, it is not mediated by an earlier colonization. Rather, it relies on the fact that, following recolonization, the adaptable species is often locally maladapted. This opens a time window for the plastic species to multiple and produce propagules before the other species becomes locally adapted, and thus competitively superior.

Introduction

A part of Ilkka Hanski's early work on metapopulation models focused on species coexistence promoted by environmental patchiness (Hanski 1981, 1983, Hanski & Ranta 1983, Hanski & Zhang 1993, Kouki & Hanski 1995), an interest that continued throughout his career (e.g., Ruokolainen & Hanski 2016). In particular, Hanski formalized and analysed Hutchinson's (1951) idea of "fugitive coexistence", in which extinction–recolonization dynamics facilitates the regional coexistence of two species, where one is a superior competitor for within-patch resources and the other is a more efficient colonizer of empty patches (Hanski 1983, Hanski & Zhang 1993). Even though the second species loses out in patches occupied by both species, its better colonization ability means that, of patches occupied by a single species, more will be occupied by it than by its competitor. This allows the competitively inferior species to produce enough propagules colonizing other empty patches before it is competitively displaced following the colonization of its patch by the competitively superior species (Hanski 1983, Hanski & Zhang 1993).

That theory is purely ecological in that it assumes that the properties of the species are fixed, with the rationale that evolutionary

changes are much slower than ecological processes. However, the last two decades brought an increased recognition that adaptive evolution can be fast, and may interact with ecological processes through eco-evolutionary feedbacks. Hanski recognized the importance of such feedbacks (e.g., Saccheri & Hanski 2006, Hanski 2012) and studied their importance in metapopulation dynamics from both empirical (Hanski 2011) and theoretical viewpoints (Zheng *et al*. 2009, Hanski *et al*. 2011). In particular, Hanski recognized that extinction–recolonization dynamics in metapopulations hinders local adaptation in heterogeneous environments in which different phenotypes are favoured in different patches (Hanski *et al*. 2011, Hanski 2012). This is because extinction obliterates locally adapted gene pools, and recolonization will often occur by propagules originating from populations adapted to other patches. Thus, even if gene flow into established populations is negligible, the degree of local adaptation is constrained: local populations need time to evolve to local trait optima, and the time available is limited by extinction. Even if a few local populations that happen to avoid extinction long enough may reach the local optima, most local populations at any time would be young and thus not yet locally adapted (Hanski *et al*. 2011, Hanski 2012). In other words, extinction–recolonization dynamics generates a "lag load" on the population mean fitness, analogous to that generated by temporal variation in the environment (Maynard Smith 1976).

The present paper links these two ideas. Using a simple metapopulation model, I show that the extinction–recolonization-generated lag load favours the coexistence of a "jack of all trades" plastic species with a species that has the genetic potential to evolve to be highly locally adapted (i.e., specialized) to the local conditions in each patch. Thus, with sufficient degree of local adaptation, the adaptable species would outcompete the plastic species in every single patch, eliminating it from the metacommunity. The extinctions and recolonization dynamics thwarts this competitive exclusion by generating new populations of the adaptable species that take time to evolve local adaptation to their freshly colonized patches, as in Hanski *et al*. (2011). This offers a time window of opportunity for the plastic species to multiply locally and produce propagules colonizing other patches before being outcompeted by the adaptable species as the latter becomes increasingly locally adapted. Thus, under this scenario, the persistence of the plastic species is of a fugitive nature, but, in contrast to the process envisioned by Hutchinson (1951) and Hanski (1983), the initial advantage does not result from a better colonization ability, but from an initial competitive advantage of the plastic species.

The model

I consider two competing species living in an environment consisting of n patches of equal sizes. One species (the adaptable one) harbours genetic variance for a quantitative trait that determines fitness, with trait optima varying between the patches. The other species is a generalist that does not show genetic variance for patch specific fitness; its fitness is assumed the same in all patches. This could be achieved through phenotypic plasticity; I thus refer to this species as the plastic species for the sake of brevity. Generations are discrete. Each individual develops to adulthood in a single patch, and both competition between the species and selection within the adaptable species occur during this stage. The outcome of competition within each patch depends on the mean relative fitness of the two species. Let q_i, denote the relative abundance of the adaptable species, defined as the proportion of the adaptable species among the newborn (i.e., before competition) in patch i ($1 - q_i$ is thus the relative abundance of the plastic species in patch i). The proportional contribution of the adaptable species to the pool of offspring produced by adults developed in patch i is then

$$q_i^* = \frac{q_i w_{\mathrm{A}i}}{q_i w_{\mathrm{A}i} + \left(1 - q_i\right) w_{\mathrm{P}i}}, \qquad (1)$$

where $w_{\mathrm{A}i}$ and $w_{\mathrm{P}i}$ stand for the mean relative fitness of the adaptable and plastic species in patch i, respectively. q_i^* can be interpreted as the proportion of the adaptable species among breeding adults weighted by their reproductive potential; both are assumed to be determined

entirely by the patch of origin, even if the individual disperses to reproduce in another patch. The total pooled reproductive output of both species from each patch is fixed (an assumption known as "soft selection"; Christiansen 1975, Spichtig & Kawecki 2004); this output is the same for all patches. However, a patch can be subject to a local extinction event that wipes out the local populations of both species; the probability of this event occurring in a given patch in a particular generation is e, and is independent among patches and generations. In the remaining patches, a fraction m of adults of both species disperse at random among all patches (including the native patch). The dispersers suffer additional mortality such that only a fraction a of them reaches a destination patch (alternatively, $1 - a$ can be interpreted as cost of dispersal in terms of fecundity or fertility). In reality, it would be unlikely for two species to be characterized by identical dispersal rates and dispersal-related mortality, but parameters m and a are assumed to be the same for both species because the focus here is on coexistence mediated by mechanisms other than differential dispersal or colonizing ability. Following the dispersal stage, the adults reproduce. With these assumptions, if the local population has not gone extinct, the expected proportion of the adaptive species among the newborn patch i in the next generation is

$$q_i' = \frac{(1-m)q_i^* + ma(1-p)\overline{q^*}}{1-m+ma(1-p)}, \qquad (2)$$

where $\overline{q^*}$ is the mean of q_i^* across the local populations (i.e., the proportional contribution of the adaptable species to the reproductive output of the entire metapopulation). If the local population goes extinct, the patch is recolonized within the same generation by propagules of both species, in proportion to their contribution to the pool of dispersing individuals, which results in $q_i' = \overline{q^*}$. This implies that the number of dispersing individuals is high enough to ensure complete patch occupancy by both species. It is also assumed that the reproductive potential of both species is high enough that a contribution of a patch to the next generation is independent of the number of generations since the patch was recolonized (i.e., the carrying capacity is reached in one generation).

The plastic species is assumed to show no additive genetic variation, but to respond to environmental cues and produce a phenotype that is at or near the patch optimum. The mean fitness of the plastic species is thus the same across patches, and equals

$$w_{\mathrm{P}i} = \exp(-c), \qquad (3)$$

where c quantifies the cost of plasticity. This could be a physiological cost of the sensory or developmental mechanisms that mediate the plasticity and/or a cost of deviating from the optimum due to unreliability of cues or random noise in the plastic response. Fitness of individuals of the adaptable species is assumed be determined by a quantitative trait x under Gaussian selection with an optimum ξ_i that varies among patches:

$$f_i(x) = \exp[-s(x-\xi)^2], \qquad (4)$$

where $f_i(x)$ is the fitness of an individual with trait value x living in patch i, and s quantifies the strength of selection. Although the adaptable species does not show plasticity, it harbours genetic variation for trait x. Thus, the mean fitness of the local population of the adaptable species $w_{\mathrm{A}i}$ in patch i equals the mean of the individual fitness $f_i(x)$. Assuming weak selection, this can be approximated as

$$w_{\mathrm{A}i} \cong f(x_i), \qquad (5)$$

where x_i is the (phenotypic and genotypic) mean of trait x of the local population in patch i. From Eqs. 3–5 it follows that the adaptable species has a competitive advantage over the plastic species in a particular patch (i.e., $w_{\mathrm{A}i} > w_{\mathrm{P}i}$) if $|x_i - \xi_i| < \sqrt{c/s}$.

Because the adaptable species harbours genetic variation for trait x, the mean of the trait in each patch evolves, whereby on the one hand selection pushes it closer to the local optimum, and on the other hand gene flow brings it closer to the overall metapopulation mean. Using again the weak selection approximation, the first of these processes can be modelled as

$$x_i^* = x_i + \frac{1}{w_{\mathrm{A}i}}\frac{\partial w_{\mathrm{A}i}}{\partial x_x} = x_i v\left[\xi_i - x_i\right], \qquad (6)$$

where v is the additive genetic variance in trait x, and x_i^* is the mean genotypic value of trait x in the local population of the adaptable species after selection and before dispersal (assuming the population did not go extinct). Assuming trait x conforms reasonably well to the classic quantitative genetic model, its mean in patch i after dispersal and reproduction becomes

$$x_i' = \frac{(1-m)q_i^* x_i^* + ma(1-q)\overline{q^*}\,\overline{x^*}}{(1-m)q_i^* + ma(1-p)\overline{q^*}}, \qquad (7)$$

where $\overline{x^*} = \sum q_j^* x_j^* / \sum q_j^*$ is the mean genotypic value of dispersing individuals (with the sum taken over local populations that did not go extinct). In patches where the local population went extinct, $x_i' = \overline{x^*}$.

The above equations fully describe the recurrence of the distribution of proportion of the two species across the patches and the mean of the focal trait in the local population of the adaptable species in each patch. It can be noted that Eqs. 2 and 7 weight the contribution of local versus immigrant offspring to the next generation, the ratio of the two weights being $(1 - m)/[ma(1 - e)]$. This allows one to reparametrize the model by eliminating parameter a: the dynamics of the system for any biologically meaningful values of m and a remains identical if one substitutes $m \rightarrow ma/[1 - m(1 - a)]$ and $a \rightarrow 1$. Thus, without loss of generality I only report results for $a = 1$. (The extinction rate parameter cannot be eliminated in the same way because, in addition to affecting the contribution of immigrants to the local patch, it also determines the number of patches subject to extinction; these patches start with the species composition and trait mean corresponding to the metapopulation mean.)

In the absence of dispersal and extinctions ($m = 0$ and $e = 0$), Eq. 7 reduces to $x_i' = x_i^*$. This means that, following Eq. 6, the population of the adaptable species in each patch will converge to the local optimum as long as there is selection ($s > 0$) and additive genetic variance for the trait ($v > 0$). It will thus attain the mean relative fitness of 1 and outcompete and exclude the plastic species in every patch as long as there is a cost of plasticity ($c > 0$). I investigated numerically how the two metapopulation phenomena of dispersal and extinction–recolonization change this result, and to what extend they allow coexistence of the plastic and adaptable species or exclusion of the latter by the former.

The numerical analysis was performed using Mathematica ver. 11. I assumed a system consisting of 101 patches with the optimal trait values ξ_i uniformly distributed between –1 and 1 (the optima were set in regular intervals of 0.02 rather than sampled at random form the distribution). Starting from the initial vectors of q_i and x_i values (*see* below), Eqs. 1–7 were iterated for each patch. A pseudorandom number generator was used to determine whether both species in a given patch should go extinct in a particular generation, with probability e; this event was independent among patches and generations. Extinction was the only stochastic element of the simulations.

The numerical analysis focused first on delineating the zones in the parameter space where the adaptable species excludes the plastic species and vice versa, and where the two species coexist. This was done by testing if, for a given set of parameter values, the system dominated by one species can be invaded by the other. To test if the adaptable species can invade, the iterations were initiated with $q_i = 0.001$ and $x_i = 0$ in all patches. The adaptable species was considered to have invaded if its mean relative abundance across patches $\overline{q}$ exceeded 0.1 or if the geometric mean of the rate of increase in mean relative abundance between generations 900 and 1000 was greater than 1. Conversely, competitive exclusion (i.e., inability to invade) was concluded if $\overline{q}$ became smaller than 10^{-6} or if the geometric mean of its rate of increase between generations 900 and 1000 was smaller than 1. These criteria were found to be reliable by numerical exploration. To test for the invasion of the plastic species, the system was first iterated for 500 generations with only the adaptive species present ($q_i = 1$) to allow the trait x to evolve to an evolutionary equilibrium between local selection and gene flow. The plastic species was then introduced at a relative abundance of 0.001 by setting $q_i = 0.999$. The conclusion of invasion versus competitive exclusion was based on criteria analogous to those used for the invasion of the adaptable species. The zones of parameter space with different outcomes were determined by searching, for given values of parameters s,

v, m, e, the minimum value of parameter c that allowed the adaptable species to invade, and the maximum value of c which allowed the plastic species to invade, where the threshold values of c were established with precision of 0.002. Iterations with $e > 0$ contained a stochastic component, but comparison of multiple runs for some parameter values indicated that the differences in the threshold values of e are small (standard deviation less than 0.01). Therefore the results presented below were obtained in a single run for a given set of parameter values; for all parameter sets the same sequence of extinction events was implemented by always seeding the pseudorandom number generator with the same initial number.

In order to gain insights into the mechanisms of coexistence of the two species, I also investigated how the two species are distributed across patches when they coexist, and how well locally adapted the adaptable species is. To do this, for a selected set of parameter values where the analysis described above predicted coexistence, I performed another series of simulations, starting from an intermediate frequency of the two species ($q_i = 0.5$) and mean trait value $x_i = 0$, and run for 3000 generations. The values of q_i and x_i in all patches for the last 1000 generations of these simulations were recorded and are reported to illustrate long-term dynamics of the system. Additional simulations starting from several different initial values established that 2000 iterations were sufficient to erase the effect of initial values of q_i and x_i.

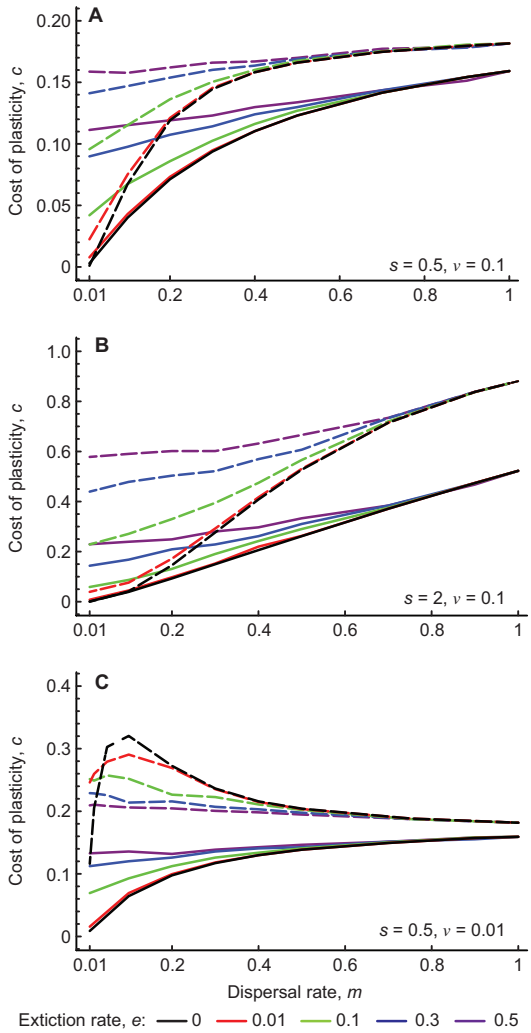

Fig. 1. The effect of dispersal rate m, cost of plasticity c and extinction rate e on the outcome of competition, at the metacommunity level, between the adaptable and the plastic species. For each extinction rate, e, the solid line shows the minimum cost of plasticity that allows the adaptable species to invade when landscape is occupied by the plastic species; the dashed line shows the maximum cost of plasticity that allows the plastic species to invade when the landscape is occupied by the adaptable species. Between the lines, the species can coexist. Panels differ in the strength of selection s and the amount of additive genetic variance in the adaptive species v.

Results

The regions of parameter space with alternative outcomes in terms of coexistence or exclusion of one or the other species are visualised in Fig. 1. The species coexist for parameter values between the solid and dashed lines of a given colour. Below the solid line, the plastic species excludes the adaptable species, whereas the opposite is true above the dashed line.

Figures 2 and 3 illustrate the properties of the equilibria with the species coexisting for several sets of parameters. The properties of equilibria are shown as the relative abundance of the adaptable species in each patch q_i, its patch-specific mean trait value x_i, and the fitness of the adaptable species, plotted as a function of the optimum trait value in the patch ξ_i.

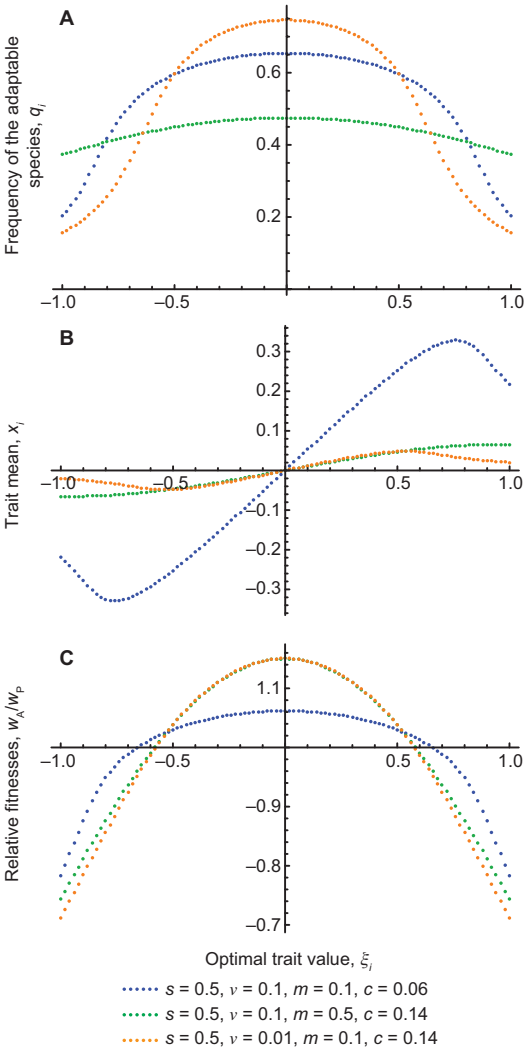

Fig. 2. Properties of the eco-evolutionary coexistence equilibrium in the absence of extinctions (e = 0), illustrated for three sets of parameter values. Patch-specific variables are plotted as a function of the optimum trait value in the patch. (**A**) The relative abundance of the adaptable species in each patch (i.e., the proportion of the adaptable species among all individuals of both species in the patch). (**B**) The mean value of trait x in the local population of the adaptable species in each patch. (**C**) The ratio of the mean fitness of the adaptable species to that of the plastic species.

The effect of dispersal in the absence of extinctions

The minimum cost of plasticity c that allows the adaptive species to invade generally increases with increasing dispersal rate m (solid lines in Fig. 1). The maximum plasticity cost that allows the plastic species to persist also increases monotonously with dispersal rate when the additive genetic variance v is high (dashed lines in Fig. 1A and B); however, when v is small, this relationship is humped (dashed lines in Fig. 1C), reaching a peak at a low m and then decreasing asymptotically. As a consequence, for high genetic variance the range of plasticity costs that allow coexistence in the absence of extinctions (i.e., the space between black lines in Fig. 1) is widest at high dispersal rates (although not necessarily maximum at m = 1), but for low genetic variance this occurs at lower dispersal rates.

This pattern results from an interaction between two effects dispersal has on the system, an evolutionary effect and an ecological (demographic) one.

The first, evolutionary effect of dispersal is to thwart local adaptation in the adaptable species through gene flow (Kawecki & Ebert 2004). This is simplest to analyse for the case when only the adaptable species is present (q_i = 1) and there are no extinctions (e = 0). As shown in the Appendix, the mean trait value at the equilibrium between local selection and gene flow in a patch with an optimum ξ_i would then be

$$\hat{x}_i = \frac{2(1-m)sv}{2(1-m)sv+m}\xi_i. \qquad (8)$$

Thus, at equilibrium, the local trait mean only corresponds to the local optimum in patches with ξ_i = 0, and deviates increasingly from the optimum the more ξ_i deviates from zero. As a consequence, the mean fitness of the adaptable species at the equilibrium is high in patches with $\xi_i \approx 0$ but is reduced in patches with ξ_i approaching ±1. Furthermore, a higher dispersal rate m results in a greater distance between the equilibrium trait mean and the optimum (except where ξ_i = 0), and thus in reduced fitness of the adaptable species. This holds qualitatively also in the presence of the plastic species, although quantitatively the mean trait deviates from that predicted by Eq. 8 as discussed below.

The second, demographic effect of dispersal is to homogenize the distributions of the species across the landscape. When both competing species are present and dispersal is low, the species become partially segregated in space such

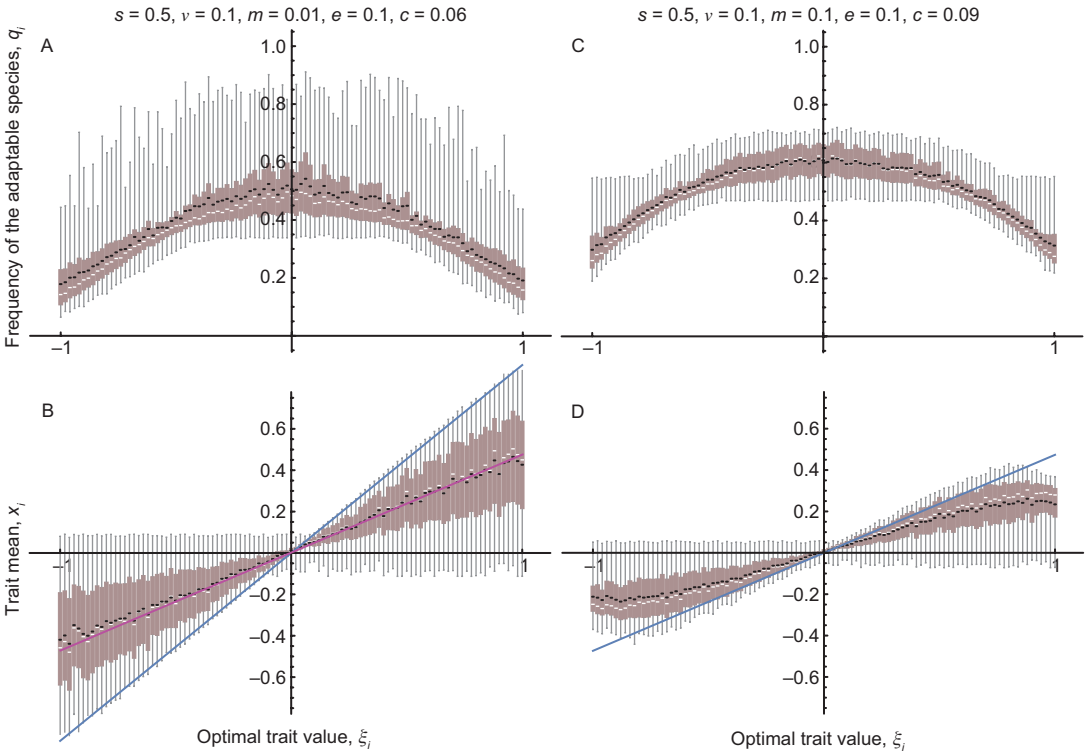

Fig. 3. Properties of the eco-evolutionary quasi-equilibrium under extinction–recolonization dynamics. The box plots show (**A** and **C**) the distribution of the relative abundance of the adaptable species, and (**B** and **D**) the meant trait values over 1000 generations in patches with different optimum trait values. The blue lines in panels **B** and **D** show the values of the trait expected if there we no extinctions (from Eq. 8).

that each becomes more abundant in patches in which it has higher fitness than the other species. Thus, the adaptable species becomes relatively more frequent in patches with ξ_i close to 0, and less frequent in patches with ξ_i approaching ±1. Dispersal counteracts this effect by mixing the two species across the landscape; thus, the species are less uniformly distributed when dispersal is lower (e.g. blue and orange dotted lines in Fig. 2A for $m = 0.1$ *versus* the green example for $m = 0.5$). Such spatial segregation, whether resulting from restricted dispersal or active habitat choice, effectively increases the importance of intra- relative to interspecific competition. This is well known to promote the coexistence of competing species (or genotypes) adapted to different habitats in heterogeneous environments (Christiansen 1975, Taper & Case 2000, Spichtig & Kawecki 2004, Ruokolainen & Hanski 2016).

Both consequences of dispersal — counteracting local adaptation homogenizing the distribution of species across the landscape — make it more difficult for the adaptable species to invade if dispersal rate is higher. This explains why the minimum cost of plasticity that allows the adaptable species to invade generally increases with dispersal rate (Fig. 1). In contrast, these two consequences of dispersal affect the invasion of the plastic species in opposite ways. When the genetic variance is high, the evolutionary effect is more important — as dispersal rate increases, the mean fitness of adaptable species in patches with ξ_i close to ±1 decreases, allowing the plastic species to invade with higher costs of plasticity (dashed lines in Fig. 1A and B). However, when genetic variance is low, even a small amount of gene flow all but erases local adaptation — the trait value remains close to zero in all patches (the orange example in Fig. 2). Further increase in dispersal rate has virtually no effect on the fitness on the adaptable species, but it continues to homogenize the distribution of the two species

across patches. This explains why the maximum cost of plasticity that allow the plastic species to persist (black dashed line in Fig. 1C) reaches a peak around $m = 0.1$ and then decreases.

These two processes interact with each other in an eco-evolutionary positive feedback. The lower relative abundance of the adaptable species in patches with ξ_i approaching ±1 magnifies the proportional contribution of immigrant genes to the local gene pool, rendering local selection on the adaptable species less effective. As a consequence, the mean trait values deviates from the optimum in those patches more than would be the case in the absence of the plastic species (Eq. 8); it may even converge towards zero as ξ_i approaches ±1 (Fig. 2B). This further impairs the fitness of the adaptable species in those patches, making it even more inferior to the plastic species (Fig. 2C), and thus further reducing its relative abundance in those patches. As a result, patches where ξ_i is close to ±1 become demographic and evolutionary sinks (Pulliam 1988, Kawecki 1995, 2008). Conversely, for the plastic species the patches with ξ_i close to ±1 become source patches and those with ξ_i close to 0 sinks. This can be seen as a special case of an interaction between interspecific competition and niche evolution described by Taper and Case (2000).

The effect of extinction-recolonization dynamics

It can be concluded from Fig. 1 that the effect of extinction-recolonization dynamics on the outcome of competition between the adaptable and the plastic species is qualitatively similar to the effect of dispersal. The minimum cost of plasticity that allows the adaptable species to invade (solid lines in Fig. 1) generally increases with extinction rate e, as it does with increasing dispersal rate m. Similarly, for the range of parameter values, for which the maximum cost of plasticity allowing the plastic species to invade increases with m, it also increases with e (dashed lines in Fig. 1A and B). Conversely, where this maximum cost decreases with increasing m, it also decreases with increasing e (dashed lines in Fig. 1C). Another parallel between the effect of dispersal and extinctions is apparent at the left-hand edge of Fig. 1C. In the absence of extinctions (black dashed line) the conditions for invasion of the plastic species are most favourable at $m \approx 0.1$ (the "peak" of the black dashed line). If extinction rate has a similar effect to dispersal rate, one would expect that for $m << 0.1$ the maximum c that allows the plastic species to invade would first increase and then decrease with extinction rate. This is indeed seen in Fig. 1C for $m = 0.01$, where intermediate extinction rates (red and green dashed lines) are most favourable for the invasion of the plastic species. The effect of extinctions vanishes as m increases, consistent with the effect of extinctions being mediated by obliterating the differentiation of local gene pools — with high dispersal this differentiation is negligible even without extinctions.

However, the effects of extinction–colonization dynamics differ in interesting ways from the effects of dispersal, as revealed by the analysis of long-term dynamics of the system. Because of the stochastic nature of extinctions and the finite number of patches, the model does not converge to an equilibrium; rather, the relative frequencies of the two species and the mean trait value of the adaptable species continue to fluctuate around a quasi-equilibrium. Properties of this attractor are illustrated by plotting the distributions of q_i and x_i in each patch over 1000 generations (Fig. 3).

The example plotted in Fig. 3A and B is for $m = 0.01$, with other parameters as for the blue example in Fig. 2. In the absence of the plastic species, Eq. 8 predicts that with these parameter values the adaptive species would evolve a high degree of local adaptation (blue line in Fig. 3B). A comparison of the box plots with the blue line in Fig. 3B indicates that the extinction–recolonization dynamics reduces the degree of local adaptation considerably; the mean trait values in patches with different optima ξ_i roughly correspond to the prediction of Eq. 8 for $m = 0.1$ (Fig. 3B, magenta line). However, in contrast to local adaptation prevented by dispersal (Fig 2B), the mean trait values of the adaptive species in Fig. 3B do not markedly deviate from the linear relationship with ξ_i as ξ_i approaches ±1. This suggest that the effects of extinction-recolonization dynamics on the distribution of the two species across habitats and its effects on

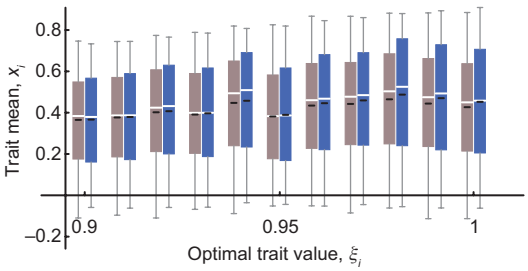

Fig. 4. Competition with the plastic species has a small effect on the degree of local adaptation of the adaptable species. The box plots illustrate the distributions of the trait value of the adaptable species in patches with the $0.9 \leq \xi_i \leq 1$ at the coexistence quasi-equilibrium for the example in Fig. 3B (brown boxes) compared to the case when plastic species is absent. Parameter values as in Fig. 3A and B.

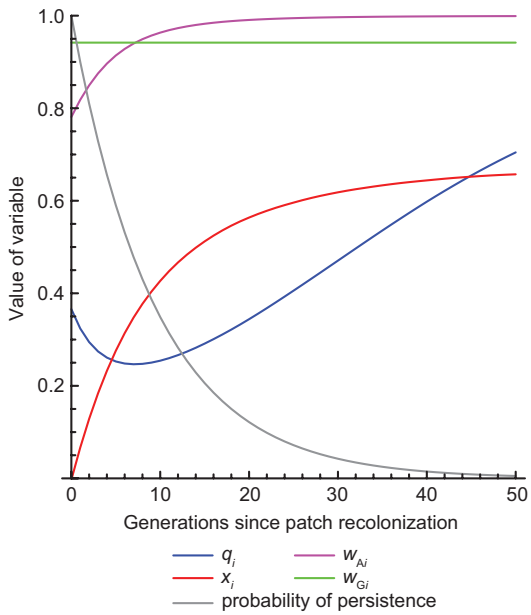

Fig. 5. An example of within-patch dynamics following simultaneous recolonization by both species. The plots show the relative frequency of the adaptable species q_i, the mean trait value x_i and the mean fitnesses of the two species, w_{Ai} and w_{Pi}, in the patch with the optimum $\xi_i = 0.7$, for the set of parameter values used in Fig. 3A and B. The grey line shows the probability of the population persisting after the set time, given the assumed extinction rate $e = 0.1$.

local adaptation in the adaptable species do not interact with each other the way the corresponding effects of dispersal do, as discussed above. In fact, even though the presence of the plastic species in the example in Fig. 3A results in the adaptable species being 2.5-fold as abundant in patches with $\xi_i \approx 0$ than in those with $\xi_i = \pm 1$, this has minimal influence on the degree of local adaptation of the adaptive species. This is visualised in Fig. 4, which directly compares the distribution of trait values x_i for the upper end of the range of ξ_i from Fig. 3B (brown boxes) with the corresponding distribution for the same parameters values but in the absence of the plastic species (blue boxes).

This is because under very low dispersal and intermediate extinction rates the degree of local adaptation is much more limited by the time available for the local gene pool to adapt (i.e., the time between colonization and extinction) than by gene flow. This is illustrated in Fig. 5, which plots the state variables of the model over time since patch recolonization for one patch (with $\xi_i = 0.7$) for the set of parameters used in Fig. 3A and B. Upon recolonization, the trait mean of the adaptable species equals the population mean (i.e., $x_i \approx 0$), which means that the adaptable species is initially locally maladapted; as a consequence, its relative abundance declines (blue line). Driven by the strong selection, the trait value (red line) evolves rapidly towards the optimum, but it still takes 8 generations until evolutionary rescue, i.e., the point when the fitness of the adaptable species (magenta line) exceeds that of the plastic species (orange line). (Recall that, based on Eqs. 3–5, this occurs when distance between x_i and the optimum becomes smaller than $\sqrt{c/s}$, which in this case means $x_i > 0.35$.) Even then, the relative abundance of the adaptable species remains below the metapopulation average (i.e., below the initial relative abundance) for another 13 generations. Throughout this time the dispersers from this patch contain a lower proportion of the adaptable species (i.e., a higher proportion of the plastic species) than the metapopulation average. This only becomes reversed after 22 generations, but with the extinction rate $e = 0.1$ assumed in this example only about 10% populations persist that long (grey line in Fig. 5). As a result, even though given enough time the adaptable species would outcompete the plastic species in this patch (and in every single patch with these parameter values), only about 30% of dispers-

ing propagules produced in this patch over its expected lifetime belong to the adaptable species. In other words, the plastic species persist because of its short-term competitive superiority following recolonization.

When dispersal rate is higher, the feedback between the demographic and evolutionary effects of dispersal does play a role, resulting in stronger reduction in the degree of adaptation in patches with ξ_i close to ±1 (Fig. 3C and D). However, the degree to which this occurs is smaller than in the blue example in Fig. 2B (which assumes the same s, v and m). Thus, the extinction–colonization dynamics to a degree counteracts the positive feedback between the demographic and evolutionary consequences of dispersal that tends to deepen the sink-like nature of patches with ξ_i close to ±1 for the adaptable species. This is because, in contrast to gene flow, the effect of extinction–recolonization dynamics on adaptation in a particular patch does not depend on the relative abundance of the two species in the affected patch.

Discussion

The model presented above reveals two eco-evolutionary feedbacks that act to promote coexistence between a jack-of-all-trades plastic species and a species that can specialize to local conditions through local adaptation in a heterogeneous patchy environment. First, gene flow counteracts local adaptation, in particular in patches where local trait optimum is at one or the other extreme of optima distributions, and thus where immigrants will bring particularly maladapted alleles. This generates a spatial refuge for the plastic species in those patches, and competition from the plastic species further negatively affects the local adaptation of the adaptable species in those patches, as discussed above. Second, extinction–recolonization dynamics results in an evolutionary lag for the adaptable species in newly recolonized patches, generating a temporal refuge for the plastic species. This promotes a fugitive persistence of the plastic species mediated not by faster colonization but by the time needed for the evolutionary rescue of the local population of the adaptable species.

As previous studies (e.g. Sultan & Spencer 2002, Hanski *et al*. 2011), the present model predicts that the generalist plastic species should be favoured in heterogeneous environments by high dispersal and/or high extinction rates. However, while those studies found that the conditions for coexistence are maximized under minimum dispersal, in the present model intermediate rates of dispersal and extinction are most favourable for coexistence. This is because in those models the coexisting species or lineages specialize on different types of patches, and thus low dispersal promotes their segregation into different patches and their local adaptation, both favouring coexistence. In contrast, the present model considers coexistence of two species which could both be generalists at the species level, one through plasticity and another through local adaptation. Given costs of plasticity, low dispersal and extinction rates would allow the adaptable species to fill every patch with a locally adapted specialized population, leaving no space for the plastic species. Thus, it is only owing to the limiting effect of gene flow and/or extinctions on local adaptation that the plastic species can profit from patches with optima far from those in most patches and/or in newly colonized patches. The evolutionary dynamics resulting from the tension between local selection and the forces disrupting it (gene flow and extinctions) also generates the frequency dependence of the competition between the species. This explains why coexistence becomes difficult at high dispersal or extinction rates and when genetic variance is low — these conditions render local selection virtually powerless, resulting in negligible local adaptation. Thus, the species coexistence in this model is inherently driven by the eco-evolutionary feedbacks.

In the model the effect of extinction–recolonization dynamics appear qualitatively similar to the effects of dispersal, as both these processes reduce the average degree of local adaptation of the adaptable species (although there are some interesting differences as discussed in the Results). Thus, there is a broad scope for coexistence in the model even without extinction–recolonization dynamics. However, this hinges upon the assumption that dispersal rate is fixed. In reality dispersal rate is affected by evolvable

morphological and behavioural traits. Extrapolating to the present model from other studies (e.g., Balkau & Feldman 1973; others reviewed in Ronce 2007), one can rather confidently conjecture that in the absence of extinctions there would be selection on the adaptable species to minimize dispersal. Evolution of lower dispersal rates would lead to an increase in the degree of local adaptation of the adaptable species, and reduce the scope for its coexistence with the plastic species (*see* Fig. 1A). This would not be predicted under extinction–recolonization dynamics, which is a powerful force selecting for an intermediate degree of dispersal (Olivieri *et al*. 1995, Ronce 2007). Thus, in the long term, extinction–recolonization dynamics would be essential to ensure the persistence of the adaptable species if dispersal rates were free to evolve.

The model makes a number of other simplifying assumptions, raising the question as to what degree the qualitative conclusions may legitimately be extrapolated to nature. In particular, one might argue that a species that performs reasonably well in all patches but is completely deprived of genetic variation that would allow it to adapt locally is biologically implausible. However, the two species considered in the model can be thought of as a special case of a pair of species where one has a lower (but not necessarily nil) potential to adapt locally in the long term but is less sensitive to being locally maladapted (e.g., owing to greater plasticity or robustness). One may thus conjecture that there is a scope for fugitive coexistence of such species. Another assumption that will often be violated is that the two species both go extinct and colonize new patches simultaneously and immediately after extinctions. Simultaneous extinctions are plausible if they are due to environmental events affecting the whole patch, such as natural catastrophes or, for parasites, the death of the host individual. However, extinctions due to demographic stochasticity could be independent or even negatively correlated between species; contrary to what is assumed here, they would also be more likely for the species that is rarer. In this case the adaptable species would be more likely to become extinct in newly colonized patches and patches with the optimum ξ_i close to ±1, whereas the plastic species would be at a greater extinction risk in old patches and those with the optimum trait ξ_i close to 0. This should facilitate coexistence by increasing the spatial separation of the two species. The assumption that patches become available for recolonization immediately after extinction is likely of minor consequence. Assuming that patches can only be recolonized some time after extinction (or that extinction results from disappearance of patches and new patches arise at random) would mainly add some stochasticity to the distribution of optima across occupied patches, and so is unlikely to have major effect in the current model. The assumption that colonization by both species occurs simultaneously is possibly more consequential, as the species that colonizes the patch first has an advantage of competitor-free space. However, as long as each of the species is equally likely to be the first colonizer (in proportion to its relative abundance across the metapopulation), this advantage should more or less average out, and the mechanisms promoting the coexistence in the model should still work.

A possibly more problematic assumption is the one of "fast demography", i.e., the assumption that a freshly colonized patch contributes as much to the pool of dispersers as a patch with a long-established local population. While this assumption greatly simplifies the analysis, it is rather unrealistic. In reality, freshly colonized patches would contribute less to the disperser pool simply because the local population sizes will be initially low. This implies that under a slower, more realistic demographic model, the plastic species would do less well — its success is mediated in part by the ability to produce propagules in the first generations after colonization. However, this would affect the contribution of the plastic species to the pool of propagules both when this species is rare and when it is common, thus presumably shifting the region of coexistence in the parameters space towards lower values of the cost of plasticity c, but not eliminating it.

Finally, the model assumes an "unstructured" metapopulation in that all patches contribute to the same single pool of dispersers which then spread equally across all patches. This implies that each patch receives the same number of immigrants and their mean trait value corre-

sponds to the metapopulation mean. This ideal scenario may be reasonably well approximated in environments in which the key ecological factors responsible for differences in trait optima show no spatial autocorrelation and each patch is connected by dispersal to multiple patches. In such a case, both the number of immigrants and their mean trait value would not correlate with the optimum in the destination patch, even if there were some isolation by distance. However, ecological factors driving local adaptation often form gradients in space. In a metapopulation on such gradient, the relative frequencies of the two species and the mean trait value among immigrants into a particular patch will no more correspond to the metapopulation mean (assuming, as is realistic, some isolation by distance). How would the predictions of the present model change if the patches were assumed to form such a gradient in space and the likelihood of dispersal between two patches to decrease with the distance between them? Compared with the unstructured environment assumed in the model, on a spatial gradient the immigrants would deviate less from the optimum in the destination patch. As a consequence, populations of the adaptable species newly re-established after an extinction event would from the start be closer to the optimum that in the unstructured case, and would tend to an equilibrium trait values closer to the optimum. This would make the invasion and persistence of the plastic species more difficult. However, as shown by Kirkpatrick and Barton (1997), an adaptable species would still be expected to evolve a cline in the trait mean that is less steep than the gradient of the optimum, with the outlying local populations being less well adapted and acting as demographic sinks. Furthermore, localized dispersal on a gradient would contribute to spatial segregation of the competing species into sections of the gradient where each does best. One can therefore conjecture that, qualitatively, there would be some scope for coexistence of the plastic and adaptable species on such a gradient, although the zone of coexistence would be shifted towards lower costs of plasticity compared with that in the unstructured model reported in this paper. Thus, although the detailed results would differ, the eco-evolutionary mechanisms mediating the coexistence in the model should extrapolate beyond the narrow set of assumptions made in the model.

This study adds support to the notion that metapopulation dynamics promotes coexistence of generalist/plastic species with habitat specialists in coarse-grained heterogeneous environments (i.e., such that an individual spends most of its life in the same habitat patch). Assuming — as is justified by empirical data and evolutionary considerations — that in its optimal habitat each specialist is competitively superior to the generalist, such coexistence is difficult to achieve under simple assumptions that lead to an equilibrium state (Brown & Pavlovic 1992, Wilson & Yoshimura 1994, Sultan & Spencer 2002, Abrams 2006, Nagelkerke & Menken 2013). Coexistence of generalists and specialists requires a mechanism that generates negative frequency-dependence, such that generalists are favored when rare but become more self-limiting as their abundance increases. Based on this and other theoretical studies, extinction–recolonization dynamics may be able to generate such a mechanism in a least four different ways. First, in the "classic" fugitive coexistence (Hanski 1983, Hanski & Zhang 1993), the advantage of a competitively inferior species comes from its higher colonization ability, meaning that on average it colonizes empty patches before its competitor. This mechanism does not require habitat heterogeneity across patches, nor that the inferior competitor has a broader niche or is more plastic. However, greater plasticity or ability to use alternative resources are one way in which a better colonization ability may be achieved: they may help dispersing individuals to survive in the "non-habitat" between patches, and to establish a new population upon arrival in a new patch. Second, Marvier *et al*. (2004) and Nagelkerke and Menken (2013) studied patch occupancy models with different habitat types; they found that generalist capable of reproducing in all types of patches may achieve a greater patch occupancy than any habitat specialist, thus producing a greater number of propagules to colonize the empty patches. Both these mechanisms increase the fraction of patches being first colonized by the generalist, and the frequency dependence results from the fraction

of unoccupied patches decreasing with increasing abundance of the generalist species. Third, when dispersal distance is limited, some patches may be too far from other patches of the same habitat to be reached by colonizers of the corresponding habitat specialist, but they may be easily colonized by a generalist that can use the intervening patches of any type as stepping stones (Buchi & Vuilleumier 2014). This may generates spatial "refugia" where the generalist species is free from competition from a locally superior specialist even though such a specialist exists elsewhere in the metacommunity. The fourth mechanism, the one operating in the present model, is qualitatively different, as it does not depend on differential colonization, but on eco-evolutionary feedbacks between extinction–recolonization dynamics, local adaptation and the distribution of the species across patches. All these mechanisms can potentially act at the same time. Taken together, this suggests that extinction–recolonization dynamics can be a powerful force favouring coexistence of species with different niche breadths and degree of specialization or local adaptation. Furthermore, the present study adds to the growing awareness that eco-evolutionary dynamics can be an important force affecting metapopulation and metacommunity dynamics, a view strongly promoted by Hanski.

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Appendix

Here I derive the equilibrium degree of local adaptation (i.e. the balance between selection and gene flow) for the adaptive species in the absence of the plastic species and under no extinctions. Setting $e = 0$ and $q_i = q_i^* = 1$ (as well as $a = 1$ as explained in the "Model" section) and replacing x_i^* in Eq. 7 with the right-hand side of Eq. 6 yields

$$x_i' = (1-m)\left[(1-2sv)x_i - 2sv\xi_i\right] + m\overline{x^*}. \tag{A1}$$

At the equilibrium, by definition, $x_i' = x_i$ for all patches. Setting $x_i' = x_i$ and solving the resulting equation for x_i yields the equilibrium mean trait value for each patch as a function of the optimum in this patch:

$$\hat{x}_i = \frac{2(1-m)sv\xi_i + m\overline{x^*}}{2(1-m)sv + m}. \tag{A2}$$

This is not a closed form solution because the right-hand side contains the post-selection metapopulation mean $\overline{x^*}$, a function of $\hat{x}_i$. However, with $q_i = 1$ for all patches, random dispersal assumed in the model does not affect the population trait mean, i.e., $\overline{x^*}$ equals the post-dispersal metapopulation mean of $\hat{x}_i$, i.e.:

$$\overline{x^*} = \frac{2(1-m)sv\overline{\xi} + m\overline{x^*}}{2(1-m)sv + m}, \tag{A3}$$

which is only satisfied if $\overline{\hat{x}} = \overline{x^*} = \overline{\xi}$. Thus, the metapopulation mean of the trait at equilibrium equals the mean of the optimum trait value across patches. When $\overline{\xi} = 0$ as assumed in this paper, $\overline{x^*} = 0$ and Eq. A2 is reduced to Eq. 8 in the main text.