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Abandoning the ship using sex, dispersal or dormancy: multiple escape routes from challenging conditions

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Natural populations often experience environments that vary across space and over time, leading to spatio-temporal variation of the fitness of a genotype. If local conditions are poor, organisms can disperse in space (physical movement) or time (dormancy, diapause). Facultatively sexual organisms can switch between asexual and sexual reproduction, and thus have a third option available to deal with maladaptedness: they can engage in sexual reproduction in unfavourable conditions (an 'abandon-ship' response). Sexual reproduction in facultatively sexual organisms is often coupled with dispersal and/or dormancy, while bet-hedging theory at first sight predicts sex, dispersal and dormancy to covary negatively, as they represent different escape mechanisms that could substitute for each other. Here we briefly review the observed links between sex, dormancy and dispersal, and model the expected covariation patterns of dispersal, dormancy and the reproductive mode in the context of local adaptation to spatio-temporally fluctuating environments. The correlations between sex, dormancy and dispersal evolve differently within species versus across species. Various risk-spreading strategies are not completely interchangeable, as each has dynamic consequences that can feed back into the profitability of others. Our results shed light on the discrepancy between previous theoretical predictions on covarying risk-spreading traits and help explain why sex often associates with other means of escaping unfavourable situations.

This article is part of the theme issue 'Linking local adaptation with the evolution of sex differences'.

1. Introduction

Natural populations often experience environmental challenges that vary across space and over time, which leads to spatio-temporal variation in fitness components of a given genotype. Spatio-temporal variation is one of the key factors promoting dispersal [1,2], but moving elsewhere is not the only way to escape a situation that may pose problems of survival or reproduction. Just like dispersal in space can spread the risks that a lineage encounters across space, 'dispersal in time'—i.e. dormancy or diapause—can perform the same task across a temporal dimension [3–5] in those organisms capable of living through unfavourable periods of time using this method.

Some organisms also have a third option available to them: a choice of whether reproduction occurs sexually or asexually. Facultatively sexual organisms (including cyclical parthenogens) often engage in sex when they encounter stressful conditions (see [6] for a recent review). To understand why sex can work somewhat analogously to dispersal or dormancy, it is useful to view each of these strategies as mechanisms with which to escape current conditions that are challenging to cope with. An organism that avoids dispersal, avoids

dormancy and avoids sex (i.e. reproduces asexually) is committed to creating exact copies of itself to use the current resources. While this can conceivably pay off when conditions are both good and unchanging, any other situation might call for risk-spreading strategies. An allele that promotes dispersal will find itself in novel spatial locations, an allele that promotes dormancy will be expressed in a new environment some time into the future, and an allele that promotes sex will find itself placed into a new, and hopefully better performing, genetic background. Thus, sex adds a 'travel in identity' option to the commonly contrasted set of travel in either space or time. This perspective on sex has been called the 'abandon-ship' principle [7–10], and predicts that organisms in poor condition should be particularly prone to choosing a sexual over an asexual life cycle. More generally, each of the 'travel' strategies can conceivably represent bet-hedging [3,11], defined as strategies that lead to beneficial reductions in fitness variance [2,12] while reducing mean fitness (reflected, respectively, in discussions of costs of sex [13], costs of dispersal, [14] and mortality during dormancy [15,16]).

Spatio-temporal environmental variation is only one of many factors that can potentially select for dispersal, dormancy or sex (for general reviews, see e.g. [17–20]). Yet, spatial and temporal fluctuations provide an interesting set of problems to a focal organism because they can be solved by 'travelling' away from a difficult situation using any of the three mechanisms—and they could also be used simultaneously. Hence, we can ask which set of mechanisms an organism is expected to employ. A general expectation from bet-hedging theory [21] is that efficient use of one method should diminish selection to employ any other. Heuristically put, it is not worth paying twice to solve a problem once.

Dispersal and dormancy as alternatives that might substitute for each other have attracted theoretical and empirical attention [3,22]. These strategies share similarities in entailing morphological or other costs (e.g. predation risk, [3], or the risk of ending up in an unknown environment, [22]). Similarly, their benefits are largely analogous [23,24], including reduced crowding [5], local competition ([25,26], but see [27]) and inbreeding [28,29]. If these strategies substitute for each other [3,23,30–34], one expects a negative correlation between them, with species or populations with stronger dormancy investing less in dispersal (evidence from plants supports this interpretation, though not without exceptions, [33]). As pointed out by Snyder [22], exceptions can occur because dispersal and dormancy are not dynamically equivalent. They possess intertwined fitness effects. If the natal habitat is good enough to have produced a newborn, it is likely better than a random site. If (in addition to spatial variation) there is positive temporal autocorrelation in habitat quality, dispersal means moving to a place that does not enjoy the statistical association between 'currently good habitat' and 'natal site'. Dormancy makes this cost smaller, as the association at home becomes weaker: waking up from a (potentially long) period of dormancy means that the past association between 'home' and 'good' has decayed. Dormancy thus effectively reduces one aspect of dispersal costs, which as a net effect can create positive covariation between dispersal and dormancy [22].

Less theoretical attention has been paid to the evolution of correlations between sex, dispersal and dormancy. But as we

review below, such patterns are amply documented, empirically. Our subsequent goal is to explicitly model covariation patterns between facultative sex, dormancy and dispersal, when investment in these strategies depends on current conditions. We highlight that the within-species patterns may differ from across-species patterns.

(a) How does sex covary with dispersal and dormancy in nature?

Observed links between dormancy and dispersal have been reviewed elsewhere [33]. We therefore focus on the co-occurrence of dispersal, dormancy and sex in facultative sexual organisms.

Sexual reproduction (in facultative sexuals) has long been reported to associate with dispersal, the formation of resistant structures or both [35–37]. In cases where one can find a clear difference in resistance to abiotic stress factors between sexually and asexually produced offspring, the sexual forms are often superior. For example, in most aphid species, sexually produced eggs are the only cold-resistant stages [38]. In the cladocerans, *Daphnia* [39,40] and *Bythotrephes* [41], sexually produced eggs undergo diapause, encapsulated in a cold- and drought-protective envelope. The same applies to cyclically parthenogenetic rotifers [42]. Oligochaete worms can reproduce asexually via fission, whereas diapausing cocoons are produced sexually and are induced in unfavourable conditions [43]. In many plants, growth can lead to vegetative propagules, whereas seeds tend to be produced sexually. Also, in those fungi that can produce both sexual and asexual spores, the former appear more environmentally resistant while asexual spores are destined to germinate quickly [44].

However, there are also exceptions. Some *Daphnia* [45] are capable of producing resting stages asexually, and apomictic plants can produce seeds asexually. Likewise, in fungi, survival structures are generally associated with sex (e.g. meiotically produced ascospores, [46]), yet species also have the ability to produce conidia, asexual survival structures that can also disperse [47]. Also, there are taxa (e.g. tardigrades [48], bdelloid rotifers [49]) where adult stages can enter an anhydrobiotic stage, that can endure extreme conditions. Finally, certain bryozoans produce statoblasts, masses of cells contained in a chitin shell, that can withstand desiccation and freezing (and can either disperse or stick to the parent colony [50]).

Positive associations between dispersal and sexual reproduction [51] are also widely observed, though we also list known exceptions to the pattern. Vegetative growth in modular organisms (e.g. many plants) can lead to offspring that can be considered independent in demographic studies [52]—runners in strawberries being a familiar example. Such offspring typically grow near their parent, while sexually produced seed may be equipped with traits that ensure dispersal. The fact that vegetative growth occurs clonally (i.e. only mitotic cell divisions between parent and offspring) may appear obvious, but it is not. No biological law prevents there to be a fertilization event somewhere among the many cells of a modular organism, followed by vegetative growth from that point onwards (i.e. it is valid to ask why strawberry runners begin growing from near the root, when they could also start from flowers). Likewise, no law states that dispersive structures cannot be formed asexually. For example, in

many fungi, a fertilized mycelium can keep dividing, taking its fertilized state—called a dikaryon—with it.

Fungal life cycles offer food for thought regarding sex and dispersal. Fungal reproduction differs markedly from an outcrossing plant's case where pollen moves to fertilize ova. In plants, this arrangement automatically associates outcrossing with at least some gene flow (though the converse, that asexuality automatically prevents dispersal, is not true: asexual plants can use apomixis to produce dispersing seeds). In fungal life cycles, sex and reproduction (the production of dispersing propagules) are not necessarily temporally or physically coupled, and this makes positive associations (e.g. yeast [53]) intriguing. Most basidiomycetes (the fungal taxon that includes mushrooms and puffballs) disperse primarily as haploid basidiospores. In mushroom-forming fungi, fertilization happens underground, where two monokaryons—haploid mycelia—meet. Fertilization leads to a dikaryon, with the dikaryotic state then spreading through existing mycelia [39]. Spores are produced by the dikaryotic mushroom. Although the continued post-fertilization growth of mycelia forms a clear contrast to plants (and bears some resemblance to our hypothetical 'runners growing from strawberry flowers' scenario), one can nevertheless state there to be some association with sex and long-distance dispersal. This association exists because dispersal through meiotically produced spores follows the underground sexual bout, though with a clear delay [54,55]. In some pathogenic fungi, sex is also required for the production of infectious spores to colonize a new host [54,56].

In lichen-forming fungi, both asexual and sexual dispersal is possible, but with different means. Asexual propagules come in various shapes and sizes that can break off and disperse from the parent organism; possible shapes include peg-like isidia, leaf-like squamules and phyllidia [57,58]. Sexually produced offspring appear designed to disperse further [59,60], with specific adaptations to take advantage of the wind. Ascospores are sexually produced propagules that only contain the fungal part of the algal–fungal symbiosis. Their active discharge into the surrounding air has earned them the name 'fungal cannons' *sensu* [61]. Lichen reproduction is thus argued to provide genetic and spatial escapes from kin competition [62].

In other fungi, the size and shape (and therefore dispersal ability) of the propagules is often dependent on the reproductive mode. Some fungi produce two types of spores: for instance, *Mycosphaerella* produces ascospores sexually and conidia asexually. While ascospores are dispersed by wind from several hundred metres to several kilometres, conidia travel by rain-splash up to a few metres only [63,64]. In yeast, the [SWI+] prion simultaneously enhances dispersal and outcrossing (by inhibiting mating type switching such that mother cells cannot mate with their daughters) [53].

In sessile and modular animals, active dispersal is often associated with a switch from vegetative to sexual reproduction [51], whereas mechanisms of passive dispersal do not require sex. In most hydroids, bryozoans, corals and polychaeta, asexual reproduction is achieved by units that separate from parents by budding, fission or by accidental fragmentation. These units may disperse passively. Active dispersal, however, is achieved by sexually produced larvae [65,66]. Similar patterns are found in sponges (Porifera), where asexual reproduction occurs by budding, gemmulation or fragmentation [67,68], leading to passive dispersal

via currents and storms [68]. Porifera sex results in the production of free-swimming, actively dispersing larvae; gametogenesis is triggered by environmental factors, e.g. temperature [67,69]. Some species of *Nemertea* (ribbon worms) can reproduce asexually through fissiparity [70]. Thus in asexual reproduction the dispersal distance is limited through adult movement, while sexually produced larvae can disperse over long distances during a pelagic phase [71].

In many Cnidaria classes (Siphonophorae [72], Trachylinae and Scyphozoa [73], Anthozoa [74]), sexually produced offspring typically engage in active dispersal [51,62]. In Ctenophora (e.g. entoprocts; commonly known as comb jellies), asexual reproduction takes place through budding. The resulting offspring can swim slowly—this group is the largest animal that swims using cilia—but dispersal distances are unknown [75]. Sexually produced larvae appear capable of longer distance dispersal, but again, exact distances are unknown [75].

Echinoderms (e.g. sea stars and sea urchins) reproduce asexually via fission. An arm or another part of the body can regrow after breaking off [76], and some species engage in active asexual reproduction where a fracture develops on the lower surface of the arm, and the arm pulls itself free from the body, which holds onto the substrate [77,78]. Larvae can disperse over much longer distances, and they are usually sexually produced and develop after broadcast spawning. Larvae can, very rarely, also arise through parthenogenetic reproduction [79]. In both main classes of Hemichordata, there is a similar pattern. Enteropneusta (acorn worms) engage in vegetative reproduction after an adult worm breaks into two, and Pteroanchia can bud asexually [80]. Both classes can also reproduce sexually and produce actively dispersing larvae.

It is also worth commenting on an analogy between selfing/outcrossing and asex/sex. Although self-fertilization is not equivalent to full asexuality, there are similarities between our question and the much better addressed botanical question of whether self-fertilization should be associated with less, or more, dispersal than outcrossing. This question has attracted interest since the 1950s, when Baker hypothesized that selfing enhances colonization success [81]. Recent theoretical work [82–84] has produced intriguingly conflicting results. Models that do allow the same individual to produce two different dispersal morphs find that dispersal ability should covary positively with outcrossing [83,84]. However, the opposite pattern becomes more likely if a plant can equip selfed seeds with different dispersal abilities than the outcrossed ones [82]; the predictions in [82] also depend on whether one assumes evolutionary constraints to play a role. For the debate regarding the validity and scope of 'Baker's Law' (selfing evolving as a reproductive assurance mechanism in colonization contexts), see Cheptou and Pannell *et al.* [85,86].

What can be said about the patterns we have uncovered as a whole? In the vast majority of the above-documented cases, the likely dispersal distances are not known to any degree of precision, nor are dormancy tendencies quantified in any systematic manner. A potential issue of any narrative account is that impressions may be disproportionately driven by a few well-studied organisms—in the related field of elucidating the benefits of sex, it has recently been pointed out that conclusions from field-based studies may be disproportionately driven by results on just three genera of small aquatic invertebrates: *Daphnia*, *Potamopyrgus* and *Campeloma*

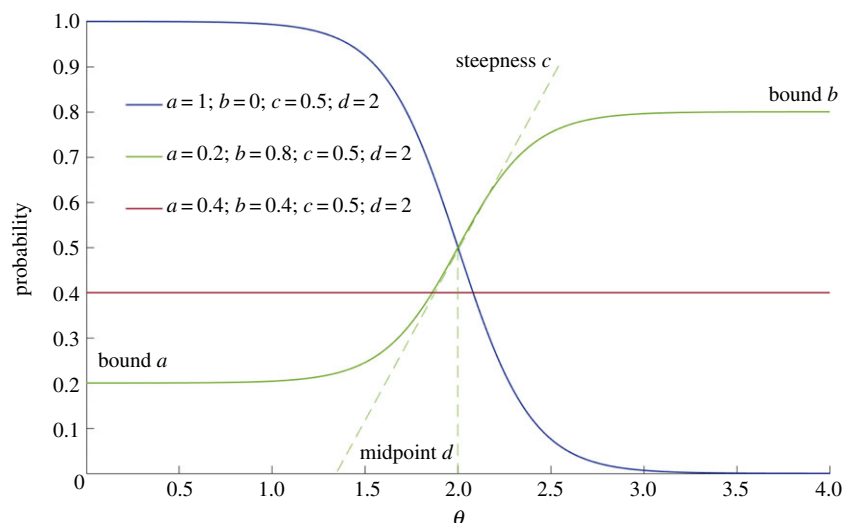


Figure 1. Example reaction norms for different combinations for a, b, c and d .

(water fleas and two different freshwater snails) [87]. Nevertheless, we believe that our narrative has identified a pattern that is so strong that exceptions probably really are exceptions: vegetative growth (with the potential for budding, i.e. short-distance dispersal) is clearly associated with mitotic cell lineages where sex does not occur, while sex very often creates dispersive propagules.

The allocation decisions, including the cues that an organism uses to begin investing in sexual reproduction, are typically also not known in any great detail—with the exception of cyclical parthenogens. Here condition-dependent investment is often documented ([7], review [6]): sex is triggered by nutrient limitation in a large number of microbial species (e.g. *Chlamydomonas* [88]) as well as in multicellular Metazoa. Increasing crowding, which typically implies reduced food availability, as well as extreme temperatures, induce male production and sex in *Daphnia* [89]. Indeed, it has been pointed out that sex becomes easy to explain if sex is a prerequisite to the production of a dormant form, and time periods that can only be survived using dormancy occur regularly [90]. The deeper question, however, is why sex should be associated with the production of such forms in the first place.

Here we model coevolutionary dynamics where populations can locally adapt to their environment, investing independently in sexual reproduction, dispersal and dormancy in spatially and temporally varying environments.

2. Model

(a) Overview

We created individual-based simulations of a population of facultatively sexual diploid hermaphrodites inhabiting a toroid-shaped world. Each individual has 13 diploid loci in total. Twelve of them result from having two alleles each for four parameters that are required to describe a logistic reaction norm for three independently evolving traits: sex, dispersal and dormancy. The alleles on the remaining locus describe an individual's phenotype in terms of its adaptedness to the current environment ('local adaptation phenotype' for short; see 'Environment' below for details).

We assume that individuals are able to measure their adaptedness to the current environment, as the degree of mismatch (denoted θ) is impacting the individual's condition. The condition is measured implicitly, with larger deviations between the current phenotype and the ideal phenotype (the one currently favoured by the environment) implying poorer condition. The reaction norms specify the probabilities that an individual with a given θ undergoes a sexual cycle, disperses and/or goes dormant, respectively. Each of these reaction norms is described by four evolving parameters, a , b , c and d (with both a and b bounded between 0 and 1), allowing a wide range of potential responses to an individual's current levels of maladaptedness, θ . Individuals can increase or decrease the probability of each response (sex, dispersal or dormancy), and options include keeping the response always highly probable, or always highly unlikely (figure 1); this is achieved by using the logistic functions for each probability

$$p_{\text{sex}} = a_{\text{sex}} + \frac{b_{\text{sex}} - a_{\text{sex}}}{1 + e^{-10c_{\text{sex}}(\theta - d_{\text{sex}})}} \quad (2.1a)$$

$$p_{\text{disp}} = a_{\text{disp}} + \frac{b_{\text{disp}} - a_{\text{disp}}}{1 + e^{-10c_{\text{disp}}(\theta - d_{\text{disp}})}} \quad (2.1b)$$

$$\text{and } p_{\text{dorm}} = a_{\text{dorm}} + \frac{b_{\text{dorm}} - a_{\text{dorm}}}{1 + e^{-10c_{\text{dorm}}(\theta - d_{\text{dorm}})}} \quad (2.1c)$$

Here θ describes the match between an individual and the state of the environment it resides in, defined such that θ is the distance to the environmental state (the locally optimal phenotype). Increasing θ implies increasing maladaptedness. The parameters are additively determined by the sum of allelic values at each locus (see 'Mode of reproduction, inheritance and mutations' for details). Note that as we do not constrain b to exceed a , nor require c or d to remain positive, the model allows individuals of low condition to evolve either higher or lower probabilities to perform an 'escape' compared with an individual in high condition.

We model soft selection such that each patch creates the same number of offspring in each generation, with better-adapted individuals (that are not currently undergoing dormancy) disproportionately represented as parents.

(b) The environment

The population inhabits a two-dimensional world of $S \times S$ discrete habitat patches, with wrapped edges (i.e. a toroid world in which moving to a smaller patch number from patch 1 along either axis leads to patch S). Each patch, characterized by coordinates i and j , has an environmental state E_{ij}^t , bounded between 0 and 1, that varies over time t . We initiated the world at time $t = 0$ by setting E_{ij}^0 as either 0 or 1 with 50% probability (no spatial autocorrelation). Spatial and temporal autocorrelation was thereafter introduced by updating the environmental state using temporal and spatial autocorrelation modifiers p_t and p_s , respectively, such that

$$E_{ij}^{t+1} = p_t(p_s \overline{E_{ij}} + (1 - p_s)E_{ij}^t) + (1 - p_t)\varepsilon \quad (2.2)$$

Here $\overline{E_{ij}}$ is the mean of the environmental states of the four neighbouring squares; ε is a uniformly distributed random number between 0 and 1 (thus if p_s is low, patches tend to deviate greatly from their neighbours; if p_t is low, the newly randomized number ε impacts the environmental state more than the recent history). Each patch has the same number of neighbours (the neighbours of 11 are S1, 1S, 12 and 21).

The resulting dynamics of the $S \times S$ grid were normalized so that the mean E_{ij}^t averaged across patches was, at all times, 0.5 with standard deviation σ , to avoid creating worlds that are inherently more difficult to adapt to in any other sense than varying the temporal and spatial rate of changes.

Optionally, each time step has patches becoming temporarily uninhabitable with probability f , independently applied to each patch. An uninhabitable patch kills all active individuals, while dormant individuals follow normal mortality rules (for dormancy), with no hatching attempts, during a period of uninhabitability. Once patches recover from being uninhabitable, their environmental state is calculated as if they never had been unsuitable. A restored patch can be recolonized through hatching of dormant eggs and/or dispersal.

(c) Initializing the population

We initialized the population by placing a total of φS^2 individuals at random locations, i.e. with uniformly distributed i and j coordinates between 1 and S . Here φ represents the number of offspring produced per patch and generation; the expected global output equals φS^2 if all patches are habitable and occupied; this value also equals the maximal number of active individuals at any given time point. Alleles were initiated with uniform distributed random numbers between 0 and 0.5 for a and b . The alleles for the local adaptation phenotype, c and d , were initiated as random numbers drawn from the standard uniform distribution on the interval (0,1) and divided by 2, such that the sum of two alleles falls between 0 and 1.

(d) Sequence of life-history events within a generation

Every generation is, without loss of generality, assumed to take 1 year (though dormant individuals can live longer) and has the following temporal order. Every year begins with a fraction τ of dormant individuals dying, regardless of their patch being uninhabitable or not. All non-dormant inhabitants of currently uninhabitable patches die. Thereafter, we examine the following events.

(i) Activation of dormant individuals; measurement of local (mal)adaptedness

On each patch, local dormant individuals can re-awaken. The number of such individuals may be limited either by the availability of dormant individuals and the rate at which they return to the active state, or by density-dependent factors limiting newcomers' ability to recruit locally. We therefore take the number of awakening individuals as the smaller number of wn_{ij} and $\varphi - N_{ij}$, where w scales the duration of dormancy (high w leads to short dormancies), n_{ij} is the number of local dormant individuals, and N_{ij} is the current number of non-dormant individuals. The choice of the awakening individuals among the local dormant ones is random.

Each non-dormant individual has its maladaptedness score θ determined as $\theta = |E_{ij}^t - T|$, where T is the sum of the individual's two alleles that determine the local adaptation phenotype.

(ii) Mode of reproduction, inheritance and mutations

Active (non-dormant) individuals opt for being in the category of sexuals with probability given in equation (2.1a); those who do not opt for sex are categorized as asexuals. However, if there is only one individual on the patch, it will reproduce asexually regardless of its traits.

We assume that a constant number of offspring (our examples use $\varphi = 10$) are produced per patch (soft selection). These offspring can be produced sexually or asexually. Given the constant number of 'offspring slots' to be filled by local reproduction, we first determine the mothers that contribute to the next generation. All individuals effectively 'compete' to be chosen as the mother of each offspring, with propensities $e^{-\theta^2}$ for sexual individuals and $\alpha e^{-\theta^2}$ for asexual ones to be chosen. This implies Gaussian stabilizing selection (better-adapted individuals are more likely to become mothers), and $\alpha = 2$ corresponds to a twofold cost of sex.

For offspring with a sexual mother, a father is chosen, with a similar procedure but now both sexual and asexual individuals have propensity $e^{-\theta^2}$ to be chosen (we thus assume that asexual hermaphrodites can participate in siring sexual young via their male function), except for the mother of the offspring, whose propensity is now 0 (i.e. we exclude selfing). Apart from no selfing, we do not change individuals' propensities based on the fecundity they have already reached, thus multiple mating is allowed both in the male and in the female role.

Asexually produced offspring are created as copies of their mother. Sexually produced offspring obey Mendelian inheritance for all traits with no linkage assumed between any of the loci. Every allele then has an independent probability μ of mutating; mutations change the allelic value to either a lower or a higher value (50% either direction) by adding normally distributed random numbers to alleles being mutated. Mutated alleles with values greater than 0.5 are set to 0.5, while negative values are set to 0, to keep the sum of two alleles bound between 0 and 1.

(iii) Dispersal and dormancy

We modelled offspring dispersal and dormancy using two approaches. In the first approach, maternal cues determined offspring behaviour. In this case, the mother's genotype (mother's θ and reaction norm parameters in equations

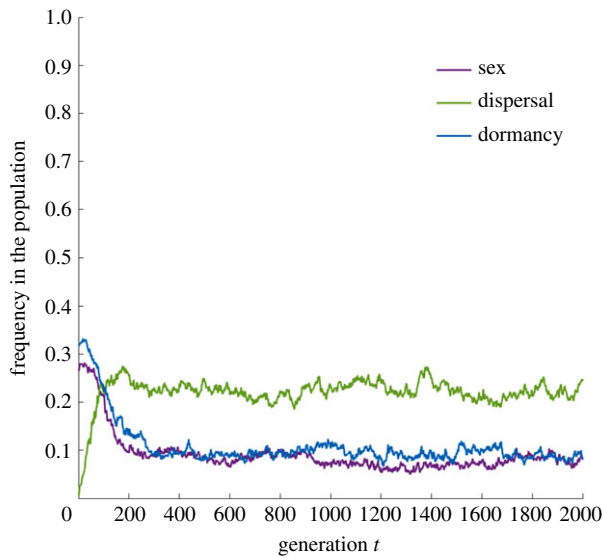


Figure 2. Example of the evolution of the mean frequency of sex, dispersal and dormancy within a population in the joint trait evolution simulations. $\alpha = 2$, $\eta = 0.1$, $\tau = 0.1$, $w = 0.8$, $D = 1$, $p_s = 0.9$, $p_t = 0.9$, $t_{\max} = 2000$, $f = 0$.

(2.1*b,c*) determined the probability of dispersal and/or dormancy of each of her offspring. In the second approach, offspring genotype underlied dispersal and dormancy decisions (based on equations (2.1*b,c*), evaluated for offspring θ and reaction norm parameters). In dispersing offspring, dormancy decisions are made after dispersal, and based on the offspring's θ in the new environment.

Dispersal is assumed risky: a fraction $1 - \eta$ of dispersers survive. Survivors are assumed to land in a random direction (any real number angle between 0 and 2π) from their original $\{i, j\}$ coordinates, with a distance drawn from an exponential distribution with mean D . An individual's new patch is determined by rounding the coordinates to the nearest integer, interpreted within the toroid geometry; thus e.g. post-dispersal coordinates of $\{7.81, 22.17\}$ are interpreted as patch $\{8, 2\}$ if the world consists of 400 patches ($S = 20$).

Equation (2.1*c*) is then applied to all offspring to determine if they go dormant (again depending either on their mother's reaction norm in the environment in which the offspring was produced or on their own reaction norm in the new environment, depending on the rule). We set a limit to the size of the 'seed bank', i.e. the bank of dormant individuals: this consists of 10 times the maximal number of active individuals. If the maximum seed bank size is reached, entering dormancy is still possible, as random dormant competitors get replaced. The rules of ending dormancy are part of the next generation, already explained above.

The offspring generation now replaces the parental one, which completes the annual cycle; the environment then changes state, and a new year begins.

(iv) Simulations

Simulations were performed for t_{\max} years, long enough to make dispersal, dormancy and sex probabilities stabilize (example shown in figure 2). We examined results (i) assuming only one escape mechanism evolves at a time (named 'constraint' simulations as two escape mechanisms are set to a fixed level) or (ii) assuming all of them coevolve ('joint evolution' simulations). In the former case, we fix two of

the three reaction norms such that there is no condition-dependence in them; practically, this is achieved by setting $a = b$ and the relevant mutation probabilities μ to 0. We then follow the evolution of the remaining trait, while varying the non-evolving traits systematically in the $\{0, 1\}$ range. In the joint evolution simulations, every trait is allowed to evolve, while we systematically vary the cost of sex ($1 \leq \alpha \leq 2.5$), cost of dispersal ($0 \leq \eta \leq 0.9$), and cost of dormancy ($0 \leq \tau \leq 0.9$) yielding a total of 120 'species' varying in all of these three parameters; we then proceeded to examine within-species and across-species patterns within this hypothetical dataset. Different species are assumed to be represented by independent runs that can differ in the costs of sex, dispersal and dormancy (and we then examine how much the species as a whole uses each of these escape mechanisms), whereas within-species patterns are examined as differential use of the escape mechanisms within a population, e.g. better-adapted individuals might use dispersal less often than poorly adapted conspecifics.

For both simulations, we report the outcomes, distinguishing between high (we use $p_s = p_t = 0.9$) or no ($p_s = p_t = 0$) spatial and temporal autocorrelations, as well as for the rule sets 'offspring decides' and 'mother decides', combined with the optional scenario where patches can become unsuitable ('ephemeral environment' scenario) or not ('continuous variation' scenario). These yield $2 \times 2 \times 2 \times 2$ options to examine (electronic supplementary material, figure S1). We report the probabilities of engaging in the three escape mechanisms (sex, dispersal and dormancy), as predicted by equations (2.1*a-c*), separately for well-adapted individuals (those with maladaptedness scores that are smaller than the global median θ_{50}) as well as for poorly adapted individuals (those with maladaptedness scores that exceed the global median). All results present averages over 10 independent runs.

3. Results

(a) 'Constraint' simulations

In the constraint scenario, one trait is allowed to evolve while the other two are varied systematically (and kept constant within each simulation run). Unless specifically mentioned, there was no qualitative difference between the 'mother decides' (figure 3) and 'offspring decides' scenario (electronic supplementary material, figure S2).

(i) Sex and dormancy decrease with dispersal rate; dormancy leads to higher dispersal

If sex is free to evolve in response to the rates of dispersal and dormancy, the frequency of sex decreases with increasing dispersal rate, with little systematic change with the rate of dormancy (figure 3*a*). There is no qualitative difference between environments with high versus no spatio-temporal autocorrelation (figure 3*a*). In all cases, the frequency of sex remains relatively low (less than 10% in the examples of figure 3*a*). Very low levels of dispersal in ephemeral environments lead to extinctions (electronic supplementary material, figure S3*a*).

The frequency of dispersal increases at high rates of dormancy, with very high dispersal rates reached when dormancy rate 1 is enforced; the rate of sex has little

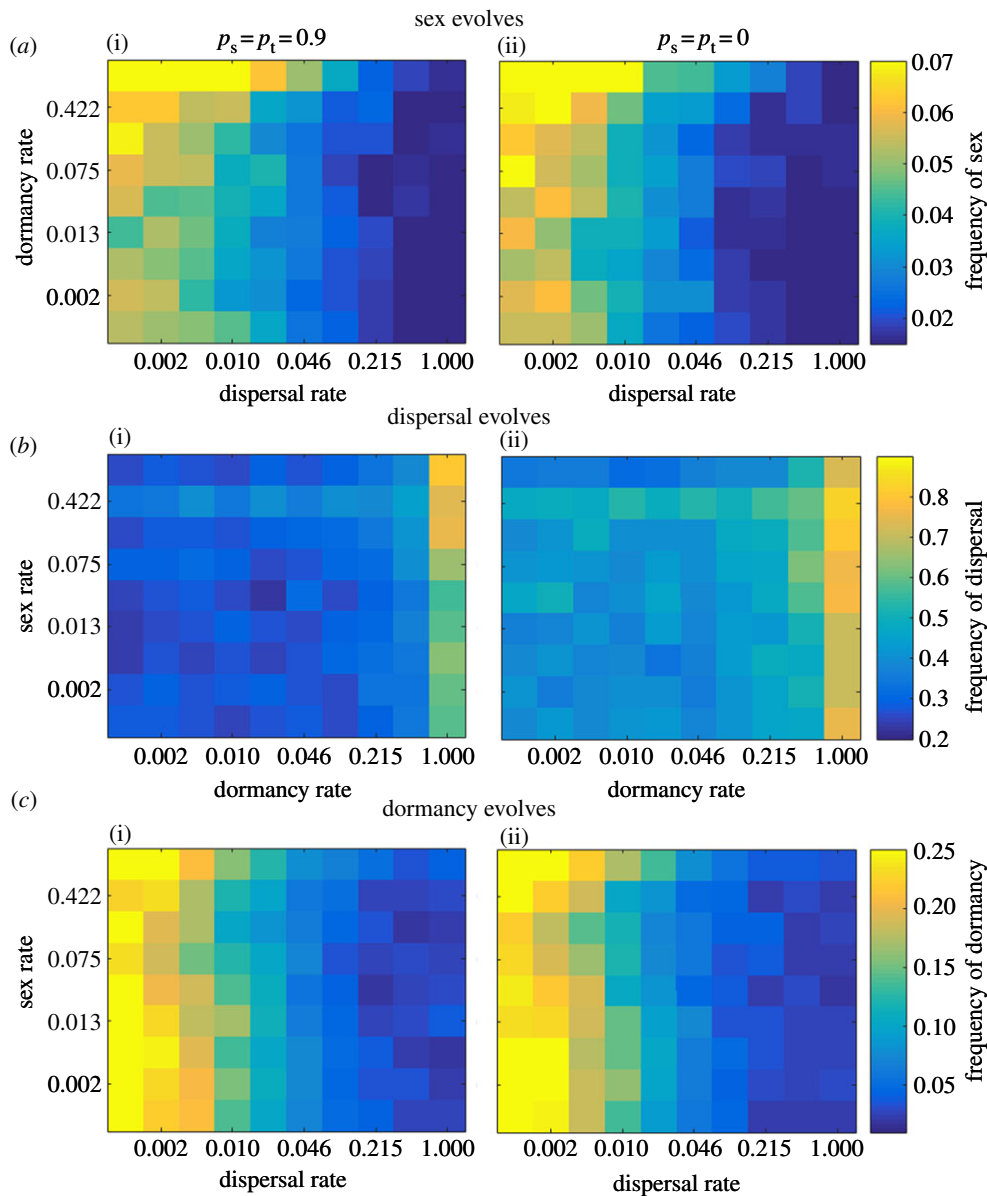


Figure 3. ‘Constraint’ simulations: Mean frequencies, measured at the end of 10 independent runs, of (a) sex, (b) dispersal and (c) dormancy, depending on the rate of the two other non-evolving traits (see electronic supplementary material, figure S2 for exact values); note the different scales on the colorbars for each trait. Panels a(i),b(i),c(i), high spatial autocorrelation; a(ii),b(ii),c(ii), no spatio-temporal autocorrelation. All figures are based on the ‘mother-decides scenario’ (see electronic supplementary material, figure S2 for ‘offspring decides scenario’) with continuous variation; $\tau = \eta = 0.1$, $\alpha = 2$, $w = 0.8$, $D = 1$.

effect on dispersal (figure 3b). This result is maintained across different spatio-temporal variation patterns, though the frequency of dispersal increases in environments with no spatio-temporal autocorrelation (i.e. fast-changing environments). Ephemeral environments, likewise, increase the frequency of dispersal compared with continuously varying environments (electronic supplementary material, figure S3b).

When the frequency of dormancy is free to evolve, we find a contrasting outcome: while dispersal evolved to be high when dormancy was kept high (discussed above), the converse is not true; dormancy evolves to be high when dispersal is *low*. Again, the rate of sex does not systematically change the pattern (figure 3c), and there is no qualitative difference between environments differing in spatio-temporal autocorrelation. The ‘continuous variation’ scenario (figure 3c) and the ‘ephemeral environment’ scenario (electronic supplementary material, figure S3c) are similar in all these respects.

(b) ‘Joint evolution’ scenario

(i) Across-species predictions: high dispersal decreases the frequency of sex and dormancy; positive covariation between sex and dormancy

Here all traits are allowed to evolve, and we vary the cost of dispersal, dormancy and sex (which presumably can vary across species in nature). The corresponding trait evolves as expected, e.g. species with the high cost of dispersal (indicated by bluer symbols in figure 4) evolve to disperse less often. Simultaneously, the cost of dispersal affects the frequency of sex and dormancy. The high cost of dispersal, by decreasing dispersal itself, increases the frequency of sex and dormancy in the population (figure 4; an expected pattern given the influence of dispersal that was forced to be high or low in figure 3). Based on figure 3, we expect dormancy to have less strong effects, unless it evolves to high rates, where it has a positive effect on sex as well as on dispersal. Indeed, very low dormancy costs can slightly increase the

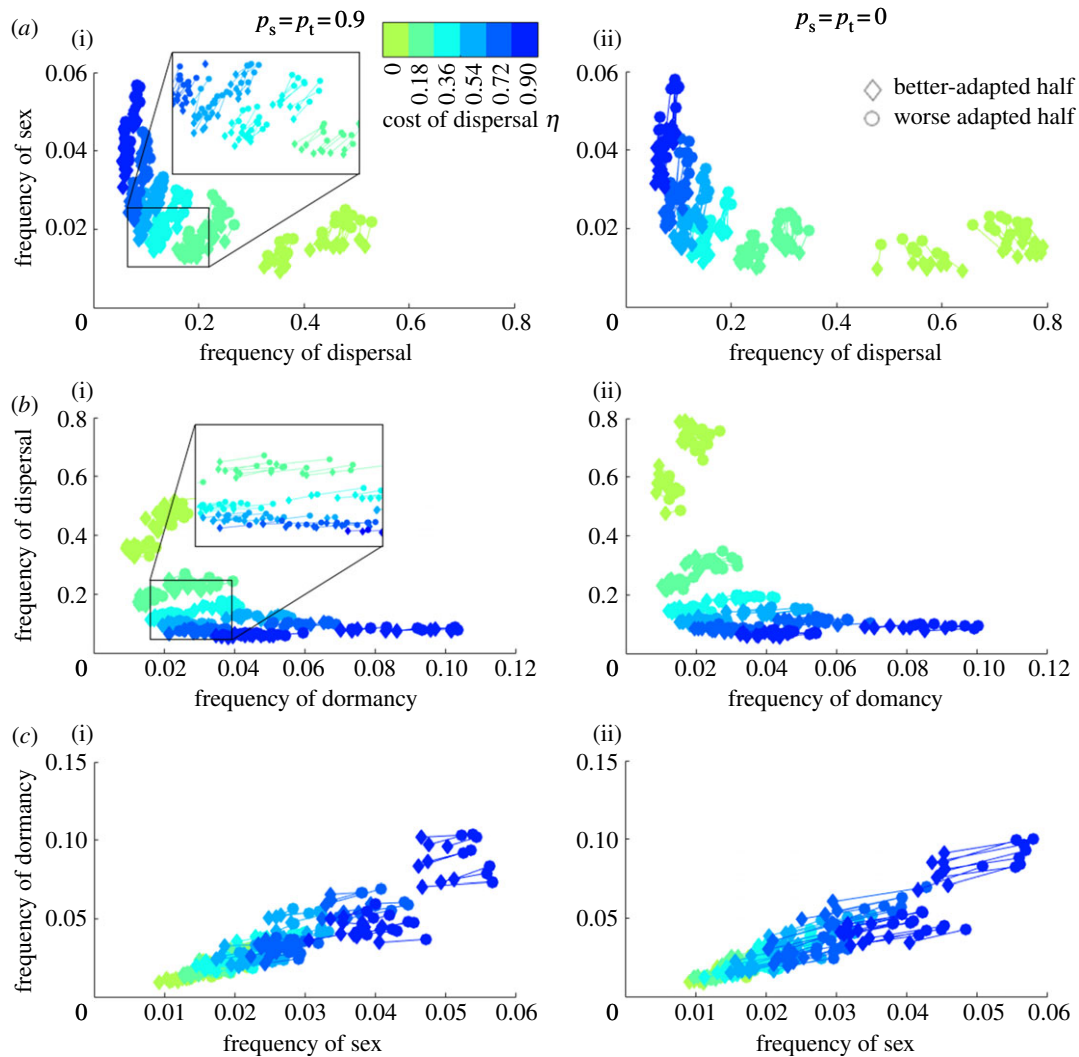


Figure 4. ‘Joint evolution’ simulations: Within- and across-population correlations of (a) dispersal and sex, (b) dispersal and dormancy and (c) sex and dormancy. Each connected pair of a diamond with a filled circle represents a population. Different populations differ in η , τ and α . The colours indicate the cost of dispersal, η (for visualizations that allow depiction of dependencies on other costs, τ or α , see electronic supplementary material, figures S6 and S4). Each symbol pair represents the better-adapted individuals (diamonds) and the poorly adapted individuals (circles). Columns indicate the different scenarios with high spatio-temporal autocorrelation (a(i),b(i),c(i)) and no spatio-temporal autocorrelation (a(ii),b(ii),c(ii)). All panels show the results for the ‘mother-decides scenario’ in continuously varying environments (see electronic supplementary material, figures S7–S9 for other scenarios). For all panels $w = 0.8$, $D = 1$ and $f = 0$.

frequency of sex as well as dispersal (electronic supplementary material, figure S4). This effect of the low cost of dormancy is even more pronounced in the ‘offspring decides’ and the ‘ephemeral environment’ scenarios (electronic supplementary material, figure S5). Based on figure 3, we can also predict that the frequency of sex has at best a mild effect on the other traits; indeed, in the joint evolution scenario, the cost of sex does not influence the frequency of dispersal or dormancy (electronic supplementary material, figure S6). Interestingly, the evolved frequency of sex itself showed much clearer responses to the cost of dispersal (figure 4) and the cost of dormancy (electronic supplementary material, figure S4) than to the cost of sex itself (electronic supplementary material, figure S6).

To phrase the findings in terms of positive and negative correlations: when comparing the frequency of sex with the frequency of dispersal across species, we find a negative relationship between the two traits, such that highly sexual species invest less in dispersal (figure 4a). Similarly, dormancy and dispersal covary negatively (figure 4b). However, the across-species patterns of the frequency of sex and the frequency of dormancy are positive (figure 4c). This appears to

be driven by the strong effect of the cost of dispersal on all traits, i.e. when costs of dispersal are prohibitive, high frequencies of sex as well as dormancy evolve to compensate.

The above statements are robust with respect to continuously varying versus ephemeral environments, (figure 4; electronic supplementary material, figures S7–S9), or scenarios where ‘mother decides’ (figure 4; electronic supplementary material, S7) or ‘offspring decides’ (electronic supplementary material, figures S8 and S9). Quantitatively, however, the ‘ephemeral environment’ scenario leads to generally higher investment in escape traits, the difference being pronounced in high autocorrelation environments (electronic supplementary material, figures S7 and S9).

(ii) Within-species predictions: condition-dependent investment leads to the positive correlation of sex, dispersal and dormancy

Across all scenarios considered, poorly adapted individuals engage more in sex, dispersal and dormancy than well-adapted individuals, leading to a within-species expectation that these traits are linked (figure 4; electronic supplementary

material, S4 and S7–S9: circles are almost invariably located more to the right, and higher, than diamonds). In special cases (at very low cost of dispersal and no spatio-temporal autocorrelation), the difference in dispersal was found to disappear or even reverse while the within-species positive correlations between sex and dormancy were maintained (note how the within-species positive correlations—the positively sloped lines connecting triangles and circles—can coexist with across-species correlations being negative, e.g. figure 4a).

4. Discussion

Our study views dispersal, dormancy and sex as three alternative (but potentially co-occurring) escape mechanisms, in the sense of the options available to an allele residing in a maladapted body: escaping spatially, temporally or genetically can all potentially restore high fitness, but each also represents a jump into the unknown. Our main finding is that the sign of the expected correlation between these three escape mechanisms can switch between within-species patterns and across-species patterns.

We discuss within-species patterns first. A previous study has, on the conceptual and empirical front, suggested that mechanistic trade-offs between the ability to disperse and the ability to go dormant create negative covariation patterns [33]. Our model is simpler in the sense of incorporating no such trade-offs, and the prediction correspondingly shifts to a positive correlation between all three traits. In the absence of a trade-off that would effectively force each individual to specialize, our model predicts that dormancy, dispersal and sex (or two of them) can be employed simultaneously.

A scenario of polymorphic specialization, where one individual goes for dormancy, another for sex and a third disperse, would require that a poorly adapted individual solves its problems via one escape mechanism so perfectly that a well-adapted individual is left to do more escaping via another means. This appears unlikely, both intuitively and according to our results. While classical bet-hedging theory can produce diversified specialists, it does not consider plasticity based on local adaptedness or condition. When responses are based on reaction norms (as in our model), our results suggest that specific individuals of one species will express an ‘escape syndrome’ that employs multiple routes at once. Cases where within-species correlations are negative (for plant and insect examples, see [33]), therefore, are conceivably indicative of trade-offs that make it difficult to possess all traits at once required for successful multi-route escaping.

All these responses are, in our model, based on condition-dependence, which assumes that organisms can perceive their own poor performance and begin employing one or more of the escape mechanisms simultaneously. If one or more of the responses is not condition-dependent (e.g. if sexual reproduction is simply triggered by mating), the coevolutionary patterns might be different, with the intriguing possibility that the organism evolves a shift to use more of the escape mechanism that can respond to the condition. We expect similar shifts to employ a particular trait (e.g. sex) more if it becomes, for any reason not included in our model, a superior way to solve a problem compared with the other two traits (e.g. dispersal and dormancy). For

example, we modelled adaptation to the current environment with one locus only, and it is known that recombination can be more strongly selected for if adaptation occurs in a multi-locus setting [91–93]. In a coevolutionary setting like ours, the effects might not be straightforward, however: a key reason why recombination ‘is more needed’ in a multilocus setting is that the ideal combination (in finite populations) is less likely to be present in an asexual population [92]. When sex is facultative, there is no separate asexual population, but asexuals can continually ‘tap into’ the sexually produced gene pool. The composition of this pool, in turn, also depends on the scale of dispersal and the frequency and duration of dormancy relative to the rates of spatio-temporal environmental variations—and on whether temporal or spatial immigrants were themselves sexually or asexually produced. It is an exciting possibility that subsequent models addressing these complications might help predict where exceptional covariation patterns might be expected.

Our way of modelling escape probabilities via three independent functions has some consequences for the interpretation. When probabilities are applied independently, populations are bound to have individuals expressing any possible combination (some show asexuality, dormancy and no dispersal; others differ in just one trait from this, etc.). Given the positive correlation emerging between them, however, we can conjecture that a pleiotropic mutation that causes two (or even three) of the phenotypic changes simultaneously, in the same reaction norm, has a chance to spread. We therefore expect adaptations that cause a switch from asex to sex while also causing survival or dispersal structures to form. Future work could usefully consider whether such pleiotropy would win over alleles causing just one reaction norm to change at a time. This, potentially together with an explicit examination of trade-offs, could shed further light on the obligateness of connections between sex and dispersal in time or space.

Turning to across-species patterns, here we showed the potential for more diverse patterns than the simplest interpretation from bet-hedging theory would predict [21]. This does not make a bet-hedging view useless: it creates the *a priori* prediction that traits *might* substitute for each other, and indeed our results confirm this can happen. Some of our predictions are, to our knowledge, novel: not only dormancy (discussed elsewhere) but also sex—when facultative—should respond to dispersal. If dispersing is, for one or another reason, difficult in a given species, its rate of sex should increase. This substitution effect (sex increases when dispersal ceases) can be so strong that the rate of sex responds much more strongly to the cost of dispersal than to the cost of sex itself. A detailed look at local adaptation can offer insight into this surprising pattern. Maximal (obligate) sex, or obligate dormancy, each lead to stronger local adaptation (shown in values of θ clustering more strongly around zero; electronic supplementary material, figure S10), than high dispersal. Thus, dispersal, with its gene flow that ‘swamps’ local adaptation [94], has stronger potential to create subpopulations with many locally maladapted individuals. If the condition threshold for sex remained unchanged, this would mean more sex; but there is now selection to shift the threshold towards less sex, as very high dispersal rates mean that the population is already maximally bet-hedging with respect to the environments that an individual encounters.

Additional heuristic insight is provided by the concept of ‘genetic time travel’ [95] in a model of bacterial transformation, where recurrent environmental change can make it beneficial for individuals to uptake DNA that arose in the past in a different lineage than their own. Costly sex in our model, likewise, appears to pay off more when some currently active individuals were born some time ago.

Thus, our results are in line with earlier work [3,22] showing that various risk-spreading strategies are not completely interchangeable: each of them has dynamic consequences that can feed back into the profitability of another. In the ‘constraint’ scenario, forcing high rates of dispersal makes the frequency of dormancy decrease (negative relationship), but the converse is not true (high dormancy leads to high dispersal; a positive relationship). Dispersing seeds risk landing in currently unfavourable patches; dormancy can reduce this cost, by spreading the germination time of these seeds [22]. However, because the response is only clear at very high dormancy rates, we do not find an increase of dispersal with the rate of dormancy (i.e. increased dispersal at low cost of dormancy in electronic supplementary material, figure S4) in the ‘joint evolution scenario’, showing that different relationships can emerge, depending on whether traits are allowed to coevolve or not.

We also briefly reviewed the wide range of taxa where sexual reproduction appears to be linked with dispersal and/or dormancy. We typically reported within-species patterns, i.e. different fates or morphologies of sexual versus asexual progeny within a species. Earlier studies linking dispersal with dormancy report mixed covariation patterns [33], with the majority of studies interpreting the question in an

across-species or across-population context. A recent study investigated the correlation of a proxy of dispersal ability (time it takes for a seed to fall in an experimental setting) and dormancy (relative germination rates) in wind-pollinated African Asteraceae species, and found a pattern suggestive of trade-offs at the individual level, but this was restricted to seed-heteromorphic species; the pattern becomes very mixed at population level which then becomes, as a whole, replaced with negative correlations at a species level [96] (see also [97]). Our results suggest that trade-offs might be responsible for cases where mothers diversify their offspring as dispersal or dormancy specialists, while within-species ‘escape syndromes’ might exist when one phenotype can efficiently perform multiple escape routes simultaneously. These predictions would be worth testing explicitly in future studies. Our results, as a whole, emphasize the message [33,96] that it is important to be explicit about the biological scale at which the question is posed, and remind us that sex, too, can be an escape route from a situation where current performance is suboptimal.

Data accessibility. The Matlab code is available on <https://github.com/nigerb/CovaCode>.

Competing interests. We declare we have no competing interests.

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