

1 **Spatial heterogeneity in the environment can favour the evolution of bet-hedging in resource**
2 **allocation to growth and reproduction**

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11 The effects of environmental heterogeneity on life history evolution have received a lot of attention.
12 Theory predicts that temporal variation in the environment favours temporal dispersion of
13 reproduction (the evolution of iteroparity; Schaffer, 1974; Tuljapurkar & Wiener, 2000; Wilbur &
14 Rudolf, 2006; but see Orzack & Tuljapurkar, 1989) and variable age at maturity (Cohen, 1966;
15 Tuljapurkar, 1990; Tuljapurkar & Istock, 1993; Menu, Roebuck, & Viala, 2000; Tuljapurkar &
16 Wiener, 2000; Wilbur & Rudolf, 2006; Koons Metcalf, & Tuljapurkar, 2008). Variation in
17 maturation age is typically achieved by a portion of offspring entering prolonged dormancy. This
18 results in ‘germ banking’ (Evans & Dennehy, 2005), for which classical examples are plant seed
19 banks (Pake & Venable, 1996). On the other hand, current theory predicts that spatial variation in
20 the environment should result in the evolution of dispersal or a combination of dispersal and
21 dormancy if the environment varies both spatially and temporally (Levin, Cohen & Hastings, 1984;
22 Cohen & Levin, 1991; Wiener & Tuljapurkar, 1994; McPeck & Kalisz, 1998; Vitalis, Rousset,
23 Kobayashi, Olivieri, & Gandon, 2013). The evolution of dispersal polymorphisms in insects is a
24 well-studied real-world example of this; the frequency of long-winged individuals capable of flight
25 is higher in unstable habitat patches, whereas short-winged flightless individuals dominate in stable

26 habitat patches (e.g. Denno, Roderick, Olmstead, & Döbel, 1991), emphasizing the effect of
27 temporal uncertainty for life history evolution in spatially varying environments. The production of
28 phenotypically diverse offspring, such as dormant and non-dormant seeds or long-winged and
29 short-winged insects, is risk spreading that ensures some fitness even if conditions turn bad. Periods
30 of low fitness have a strong negative effect on cross-generation fitness, but the production of
31 phenotypically diverse offspring reduces variance of fitness across generations, and so increases
32 long-term fitness (Dempster, 1955; Gillespie, 1977). Such risk spreading is called evolutionary bet-
33 hedging (Seger & Brockmann, 1987; Starrfelt & Kokko, 2012).

34

35 In theoretical work, the scale of environmental variation is often specified as the size of the
36 environmental ‘grain.’ In a fine-grained environment, individuals may experience a mixture of
37 environmental states during their lifetime, while in a coarse-grained environment the environment
38 remains constant during an individual’s lifetime but may change across generations (Starrfelt &
39 Kokko, 2012). Fine-grained environmental variation typically refers to spatial variation in the
40 environment, whereas temporal environmental variation is often considered as coarse-grained (see
41 Seger & Brockmann, 1987; Starrfelt & Kokko, 2012).

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43 Environmental uncertainty may favour not only the production of phenotypically diverse offspring
44 but also simultaneous resource allocation to growth and reproduction within the lifetime of an
45 individual. In perfectly predictable environments, determinate growth with a sudden switch from
46 growth to reproduction maximizes fitness (Ziołko & Kozłowski, 1983; Perrin & Sibly, 1993).
47 Temporal variation in mortality risk or offspring reproductive value, or size-dependency of
48 mortality risk, may change the optimal resource allocation so that resources are allocated to both
49 growth and reproduction after maturation, resulting in indeterminate growth (King & Roughgarden,
50 1982; Perrin & Sibly, 1993; Taylor & Gabriel, 1993; Gurney & Middleton, 1996; Wong & Ackerly,

51 2005; Ejsmond, Czarnołęski, Kapustka, & Kozłowski, 2010). In long-lived organisms, allocation to
52 both growth and reproduction after maturation is a bet-hedging strategy in response to temporal
53 variation in the environment, and results in iteroparity. However, growth also continues after
54 maturation in many short-lived (e.g. annual) organisms that produce dormant offspring, for example
55 annual plants and cladocerans (Ejsmond, Kozłowski, & Ejsmond, 2019). The production of dormant
56 offspring spreads the risk for temporal environmental uncertainty in these species, so it seems
57 unlikely that simultaneous allocation to growth and reproduction would have evolved in relation to
58 temporal environmental variation. While plant-herbivore arms race can explain simultaneous
59 allocation to growth and reproduction in annual plants (Janczur, 2009), current theory does not
60 provide an explanation for the evolution of mixed allocation to growth and reproduction in short-
61 lived animals that produce dormant offspring.

62
63 To address the evolution of growth that accompanies reproduction in short-lived organisms,
64 Ejsmond et al. (2019) developed an elegant life-history model – published in this issue of
65 *Functional Ecology* – where mortality risk varies spatially among habitat patches and the modelled
66 organism is unable to infer the ambient mortality risk. Their analysis is coarse-grained, with each
67 individual experiencing a constant mortality risk during its lifetime because they stay in the same
68 habitat patch for their whole lives. Offspring disperse among habitat patches in the beginning of
69 each of the non-overlapping generations so that part of the offspring may experience a different
70 mortality risk than the parent (only females are considered in the model). The authors ran
71 evolutionary simulations to analyse the evolution of resource allocation to growth versus
72 reproduction. They found that simultaneous allocation to both growth and reproduction after
73 maturation evolves when more than 70% of the habitat patches are risky. Growth accompanying
74 reproduction seems to be favoured in risky environments because high mortality risk selects for
75 early maturation. On the other hand, survival of a female over a longer period of time in the

76 simulations suggests that the female in question resides in a safe habitat patch where it pays off to
77 allocate resources to growth to increase body size, and thus fecundity, later in life. In spatially
78 homogenous environments and environments where most habitat patches are safe, their model
79 predicts the evolution of determinate growth, with resource allocation suddenly and completely
80 switching from growth to reproduction at maturation. This prediction is consistent with earlier work
81 (cf. Ziołko & Kozłowski, 1983; Perrin & Sibly, 1993).

82

83 Ejsmond et al. (2019) conducted their study using a metapopulation of short-lived organisms as a
84 model system, but I believe that their predictions are more general. Their analysis is coarse-grained,
85 with each individual experiencing only one environmental state during its lifetime. Therefore, it
86 seems likely that the prediction for the evolution of simultaneous allocation of resources to growth
87 and reproduction would hold in any coarse-grained environment whenever there is a high
88 probability that a newborn individual ends up in a dangerous environment and has no possibility to
89 escape the high mortality risk in space or time during its lifetime. This prediction should be most
90 applicable to short-lived organisms (Ejsmond et al., 2019). The take-home message from Ejsmond
91 et al. (2019) is that spatial heterogeneity can favour the evolution of such bet-hedging strategies that
92 traditionally were thought to evolve only in response to temporal variation.

93

94 Future studies should address whether similar bet-hedging strategies as those predicted by Ejsmond
95 et al. (2019) could evolve also in other kinds of organisms and/or fine-grained environments under
96 some conditions. More generally, it is evident that despite decades of theoretical investigations of
97 adaptations to heterogeneous environments we still do not have a comprehensive understanding of
98 evolutionary consequences of environmental heterogeneity, although life history theory is generally
99 well-established and powerful (Stearns, 1992; Roff, 2002). Further development of life history
100 theory by approaching the evolution of bet-hedging strategies from novel points of view – and

101 inspired by empirical observations – appears a fruitful avenue for future research, as demonstrated
102 here by Ejsmond et al. (2019). Numerical simulations are often required when analysing the
103 evolution of bet-hedging strategies, but such analyses are currently more feasible than ever before
104 owing to the presently available computing power.

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113 **References**

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