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Altruism in a volatile world

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The evolution of altruism – costly self-sacrifice in the service of others – has puzzled biologists since *The Origin of Species*[1]. For half a century, attempts to understand altruism have been built on the insight that altruists may help relatives to have extra offspring in order to spread shared genes[2]. This theory – known as inclusive fitness – is founded on a simple inequality termed 'Hamilton's rule'[2]. However, explanations of altruism have typically ignored the stochasticity of natural environments, which will not necessarily favour genotypes that produce the greatest average reproductive success[3,4]. Moreover, empirical data across many taxa reveal associations between altruism and environmental stochasticity[5–8], a pattern not predicted by standard interpretations of Hamilton's rule. Here, we derive Hamilton's rule with explicit stochasticity, leading to novel predictions about the evolution of altruism. We show that altruists can increase the long-term success of their genotype by reducing the variability in the number of offspring produced by relatives. Consequently, costly altruism can evolve even if it has a net negative effect on the average reproductive success of related recipients. The selective pressure on volatility-suppressing altruism is proportional to the coefficient of variation in population fitness, and is therefore diminished by its own success. Our results formalise the hitherto elusive link between bet-hedging and altruism[4,9–11], and reveal missing fitness effects in the evolution of animal societies.

The widespread phenomenon of organisms paying costs to help others (altruism) is a long-standing paradox in biology[1,2]. Recently, variance-averse investment in stochastic environments (bet-hedging) has been suggested as an explanation for a number of major puzzles in the evolution of altruism, including: (i) the origins of sociality in birds[9,11,12], insects[13] and rodents[14]; (ii) the altitudinal distribution of eusocial species[7]; and (iii) the evolution of cooperation between eusocial insect colonies[15]. The global distribution of animal societies is linked to environmental stochasticity[4]. In birds[6,12], mammals[16], bees[7]

and wasps[8], cooperation is more common in unpredictable or harsh environments. However, the effects of stochasticity have largely been omitted from social evolutionary theory. There are a handful of notable exceptions: Grafen[17] argues that selection will maximise expected inclusive fitness under uncertainty; Uitdehaag[18] shows that mutualism between nonrelatives could counteract kin selection by dampening stochasticity; and Lehmann & Rousset[19] explore stochastic effects on reproductive value. However, despite speculation[11,20], the proposed link between bet-hedging and altruism[9] has remained elusive[4]. We resolve this link by presenting a stochastic generalisation of Hamilton's rule ('stochastic Hamilton's rule'), which predicts when organisms should pay a cost to influence the variance in their relatives' reproductive success.

We allow environmental state π to fluctuate among the possible states Π; 'stochasticity' is the condition that states are unpredictable. We follow the established method of capturing fitness effects as regression slopes[1]. Both the fitnesses w_x of individual organisms and the average fitness $\bar{w}$ in the population may vary among the states Π. We denote the kth central moment of $\bar{w}$ as $\ll^k \bar{w} \gg$. The joint distribution of the fitness of individual x (w_x) and $\bar{w}$ across states Π is captured by their mixed moments (covariance $k=1$, coskewness $k=2$, cokurtosis $k=3$, etc.; *Appendix A1*). Altruists may alter not only the expected number of offspring (mean, $k=0$), but may reduce the variation in offspring number (variance, $k=1$) or increase the likelihood of large numbers of offspring (skew, $k=2$). We denote the actor's effect on the recipient's expected number of offspring as the benefit b_μ, the actor's effect on its own expected number of offspring as the cost c_μ, and relatedness as r. Likewise, we denote the actor's effect on the kth mixed moment defining the recipient's reproductive success as b_k, and the actor's effect on the kth mixed moment of its own reproductive success as c_k. The stochastic Hamilton's rule is therefore:

$$r \cdot \overbrace{\left(b_\mu + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} (\ll^k \bar{w} \gg b_\mu + b_k) \right)}^{B} > $$

$$\underbrace{c_\mu + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} (\ll^k \bar{w} \gg c_\mu + c_k)}_{C}$$

$$(1)$$

Empirical tests of Hamilton's rule have looked for benefits and costs constituting effects on the average reproductive success of recipients and actors, using the form $rb_\mu > c_\mu$ (henceforth, 'means-based Hamilton's rule')[21]. However, Inequality (1) reveals that b_μ is a single component of a spectrum of

potential benefits of altruism. Conclusions based on mean reproductive success (b_μ and c_μ) overlook effects on the variance of the distribution from which a recipient samples its reproductive success.

Asocial bet-hedging has been analysed extensively[3], and is typically described in terms of costs and benefits: the cost is a reduction in mean reproductive success, whilst the benefit is a reduction in the variance of reproductive success[3]. Following speculation that these benefits and costs could be accrued by different partners[9,13] – actors pay costs whilst recipients derive benefits (Fig. 1a) – we refer to decoupled benefits and costs as 'altruistic bet-hedging'. We let b_σ and c_σ denote, respectively, the effects on the recipient and actor's standard deviation ('volatility') in reproductive success (weighted by its correlation with population average reproductive success $\bar{w}$; for details see *Extended Data* Table E1). We introduce the 'stochasticity coefficient' v as the coefficient of variation in $\bar{w}$ across environmental conditions ($v = \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}$; Fig. 1b). Where the actor can affect both the mean and the volatility (but not higher moments) of the recipient's reproductive success, Inequality (1) simplifies (*Appendix A2*) to:

$$r(b_\mu + v b_\sigma) > c_\mu + v c_\sigma$$

$$(2)$$

Reducing the ($\bar{w}$-correlated) volatility in the recipient's number of offspring ($b_\sigma > 0$) confers on recipients greater *relative* fitness in poor environmental states: extra offspring are disproportionately valuable when competitors produce few offspring[22], underscoring the principle that the ultimate currency for benefits and costs under stochasticity is the expectation of relative fitness[1]. It is straightforward to derive the established asocial bet-hedging model[3] by setting $r=0$ (*Appendix A3*).

Formally, we define altruistic bet-hedging as a reduction in a recipient's reproductive volatility (positive b_σ) that overcomes an otherwise-deleterious cost to the actor's mean fecundity (positive c_μ). Strong benefits can arise when b_μ and b_σ are both positive. Reductions in the actor's own reproductive volatility ($c_\sigma < 0$) diminish total costs (Fig. 2a & b). Moreover, when $b_\sigma > c_\sigma$, increasing stochasticity reduces the minimum relatedness (r) required for altruism to evolve (Fig. 2c). Fluctuations in relatedness (r) alter selection only if they correlate with strong fluctuations in population average reproductive success ($\bar{w}$) (see *Appendix A4*).

We note four predictions of the stochastic Hamilton's rule that differ from standard expectations:

1. Selection can favour altruism ($C>0$) with zero increase to the recipient's mean fecundity ($b_\mu=0$). Such a seemingly paradoxical lack of benefits is observed where additional helpers appear redundant[23]. Paradoxical helpers can be selected for by reducing the recipient's reproductive volatility if:

$$rb_\sigma > \frac{c_\mu}{v} + c_\sigma$$

(3)

2. Actors may be selected to harm the average reproductive success of their relatives ($b_\mu < 0$, $c_\mu > 0$). The harm is outweighed by a reduction in the recipient's reproductive volatility (Fig. 2) if:

$$rb_\sigma > \frac{c_\mu - rb_\mu}{v} + c_\sigma$$

(4)

3. Altruists that reduce their recipients' reproductive volatility can be favoured by selection in the absence of environmental stochasticity, but only when population size (N) is low (in extremely small populations[3] or small demes with negligible dispersal[24]). Effects on variance, σ^2, not volatility, are used here for notational convenience (*Appendix A5*):

$$r\left(b_\mu + \frac{b_{\sigma^2}}{N\mathbb{E}_\pi[\bar{w}]}\right) > c_\mu + \frac{c_{\sigma^2}}{N\mathbb{E}_\pi[\bar{w}]}$$

(5)

4. Very strong altruistic effects ($b_\sigma \gg 0$) can undermine the success of the altruist genotype (*Extended Data* Fig. E1; *Appendix B1–4*). Altruists that substantially reduce their recipients' reproductive volatility spread rapidly. As successful altruists reach high frequencies, the coefficient of variation in average reproductive success ($v = \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}$) tends towards zero (*Extended Data* Fig. E2). When v is small, any b_σ has a small effect (Inequality (2)), so altruistic bet-hedgers undermine the condition (high v) that favoured them (*Extended Data* Fig. E1a&b). This frequency-dependence can generate polymorphisms of altruists and defectors (*Extended Data* Fig. E1c), provided that allele frequency does not fluctuate intensively, which can otherwise destabilise the equilibrium (*Extended Data* Fig. E3) and lead to fixation[25].

Apparent reduction of recipient reproductive volatility (implying $b_\sigma > 0$) has been shown in starlings[9], sociable weavers[26], woodpeckers[10], wasps[27], and allodapine bees[13]. We illustrate a volatility-reduction route to sociality with two examples. First, we consider sister–sister cooperation in facultatively-social insects (as in certain carpenter bees, where a means-based Hamilton's rule is violated[28]). In strongly stochastic environments, altruism can evolve between haplodiploid sisters when values of mean fecundity alone would predict it to be deleterious, as predicted by Inequality (2) (Fig. 3a) and simulations of haplodiploid populations (Fig. 3b; *Appendix C1*). Second, using published estimates of mean fecundity and high stochasticity in Galapagos mockingbirds (*Mimus parvulus*), we indicate how

volatility effects could favour cooperative breeding even if helping increases the recipient's average fecundity only as much as it reduces the actor's ($c_\mu=b_\mu$; Fig. 3c; *Appendix C2*).

Inequality (2) reveals three core conditions for altruistic bet-hedging. First, members of the non-altruistic genotype suffer synchronous fluctuations in lifetime reproductive success driven by environmental state (high v) that can be stabilised by sociality ($b_\sigma>0$). Second, relatedness (r) is above the threshold $r*=\frac{c_\mu+vc_\sigma}{b_\mu+vb_\sigma}$. Third, actors either cannot predict environmental fluctuations or cannot generate phenotypes for different conditions (Fig. 4; *Appendix B5*). If actors can obtain and utilise information at sufficiently low costs (rendering the environment predictable), plastic cooperation outcompetes constitutive cooperation (increasing b_μ and reducing c_μ).

Synchronous fluctuations (high v) are generated when different patches within the population experience correlated environmental changes (Fig. 1b; *Appendix A6*). If offspring disperse across environmentally uncorrelated patches[3] but compete at a whole-population level, v falls. Likewise, iteroparity and long generations across different environmental conditions reduce v, whilst correlated exposure to environmental conditions within lifetimes increases v. For these reasons, Inequality (2) suggests that the most promising avenues to detect b_σ-driven sociality may occur among social microbes, which can experience: (i) population-wide fluctuations (high v); (ii) short generations (high v); (iii) competing clones (high r); and (iv) opportunities to confer homeostasis on others ($b_\sigma>0$), including through the construction of biofilms[29] and incipiently-multicellular clusters withstanding profound abiotic and biotic stress.

We have shown that altruistic effects on recipient volatility are visible to selection. Significantly, Hamilton's rule identifies ultimate payoffs by incorporating any effects of population structure[1]. To make case-specific predictions, researchers should, accordingly, utilise explicit information on population structure and ecology. The empirical challenge to detect volatility-suppressing sociality in wild organisms will best be met using tailored models guided by field data for specific scenarios, led by the general framework of inclusive fitness theory[1,21,30]. In summary, Hamilton's rule reveals the action of selection under stochasticity: shielding relatives from a volatile world can drive the evolution of sociality.

Acknowledgements

Author Contributions

PK conceived the idea; PK and ADH performed the modelling; ANR and SS supervised the project. All authors discussed the ideas and wrote the manuscript.

Author Information

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Data availability

Simulation output was generated using MATLAB code provided in *Appendix D* of the Supplementary Information; these are also available from the corresponding author on request.

References

1. Gardner, A., West, S. A. & Wild, G. Thse genetical theory of kin selection. *J. Evol. Biol.* **24,** 1020–1043 (2011).
2. Hamilton, W. D. The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7,** 1–16 (1964).
3. Starrfelt, J. & Kokko, H. Bet-hedging – a triple trade-off between means, variances and correlations. *Biol. Rev.* **87,** 742–55 (2012).
4. Cockburn, A. & Russell, A. F. Cooperative breeding: a question of climate? *Curr. Biol.* **21,** R195-7 (2011).
5. Rubenstein, D. R. & Lovette, I. J. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17,** 1414–9 (2007).
6. Jetz, W. & Rubenstein, D. R. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21,** 72–78 (2011).
7. Kocher, S. D. *et al.* Transitions in social complexity along elevational gradients reveal a combined impact of season length and development time on social evolution. *Proc. R. Soc. B* **281,** 20140627 (2014).

8. Sheehan, M. J. *et al.* Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol. Lett.* **18,** 1057–1067 (2015).

9. Rubenstein, D. R. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl. Acad. Sci. U. S. A.* **108,** 10816–10822 (2011).

10. Koenig, W. D. & Walters, E. L. Temporal variability and cooperative breeding: testing the bet-hedging hypothesis in the acorn woodpecker. *Proc. R. Soc. B* **282,** 20151742 (2015).

11. Shen, S., Emlen, S. T., Koenig, W. D. & Rubenstein, D. R. The ecology of cooperative breeding behaviour. *Ecol. Lett.* **20,** 708–720 (2017).

12. Griesser, M., Drobniak, S. M., Nakagawa, S. & Botero, C. A. Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biol.* **15,** 1–17 (2017).

13. Stevens, M. I., Hogendoorn, K. & Schwarz, M. P. Evolution of sociality by natural selection on variances in reproductive fitness: evidence from a social bee. *BMC Evol. Biol.* **7,** 153 (2007).

14. Ebensperger, L. A. *et al.* Mean ecological conditions modulate the effects of group living and communal rearing on offspring production and survival. *Behav. Ecol.* **25,** 862–870 (2014).

15. Sumner, S., Lucas, E., Barker, J. & Isaac, N. Radio-tagging technology reveals extreme nest-drifting behavior in a eusocial insect. *Curr. Biol.* **17,** 140–5 (2007).

16. Lukas, D. & Clutton-Brock, T. Climate and the distribution of cooperative breeding in mammals. *R. Soc. Open Sci.* **4,** 160897 (2017).

17. Grafen, A. Optimization of inclusive fitness. *J. Theor. Biol.* **238,** 541–63 (2006).

18. Uitdehaag, J. C. M. Bet hedging based cooperation can limit kin selection and form a basis for mutualism. *J. Theor. Biol.* **280,** 76–87 (2011).

19. Lehmann, L. & Rousset, F. The genetical theory of social behaviour. *Philos. Trans. R. Soc. B Biol. Sci.* **369,** 1–18 (2014).

20. Koenig, W. D., Dickinson, J. L. & Emlen, S. T. in *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* 353–374 (Cambridge University Press, 2016).

21. Bourke, A. F. G. Hamilton's rule and the causes of social evolution. *Phil. Trans. R. Soc. B* **369,** 20130362 (2014).

22. Grafen, A. Developments of the Price equation and natural selection under uncertainty. *Proc. R. Soc. B* **267,** 1223–1227 (2000).

23. Dickinson, J. L. & Hatchwell, B. J. in *Ecology and Evolution of Cooperative Breeding in Birds* (eds. Koenig, W. D. & Dickinson, J. L.) 48–66 (Cambridge University Press, 2004).

24. Lehmann, L. & Balloux, F. Natural selection on fecundity variance in subdivided populations: kin selection meets bet hedging. *Genetics* **176,** 361–77 (2007).

25. Lande, R. Expected relative fitness and the adaptive topography of fluctuating selection. *Evolution* **61,** 1835–1846 (2007).

26. Covas, R., Du Plessis, M. A. & Doutrelant, C. Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.* **63,** 103–112 (2008).

27. Wenzel, J. W. & Pickering, J. Cooperative foraging, productivity, and the central limit theorem. *Proc. Natl. Acad. Sci.* **88,** 36–38 (1991).

28. Rehan, S. M., Richards, M. H., Adams, M. & Schwarz, M. P. The costs and benefits of sociality in a facultatively social bee. *Anim. Behav.* **97,** 77–85 (2014).

29. Lowery, N. V., McNally, L., Ratcliff, W. C. & Brown, S. P. Division of labor, bet hedging, and the evolution of mixed biofilm investment strategies. *MBio* **8,** e00672-12 (2017).

30. Birch, J. The inclusive fitness controversy: finding a way forward. *R. Soc. Open Sci.* **4,** 170335 (2017).

Figure Legends

Figure 1 | Environmental stochasticity has been missing from models of social evolution. In the non-stochastic application of Hamilton's rule to real-world organisms[21] ($rb_\mu > c_\mu$), recipients gain an increase in average reproductive success ($b_\mu > 0$) whilst actors suffer a decrease in average reproductive success ($c_\mu > 0$). **(Panel a)** We formalise an explicitly-stochastic Hamilton's rule: $r(b_\mu + vb_\sigma) > c_\mu + vc_\sigma$. This shows that benefits can also arise by reducing the volatility of the recipient's reproductive success ($b_\sigma > 0$), which depends on the magnitude of environmental stochasticity (v). An increase in the actor's reproductive volatility ($c_\sigma > 0$) imposes a cost on the actor. Each effect represents a transformation of a probability distribution for reproductive success (lower element of panel). Total benefits and costs (B and C) are measured in expected relative fitness[1]. **(Panel b)** Environmental stochasticity (v) is highest when spatial patches fluctuate in sync: for instance, if drought affects a randomly-chosen patch Z, it should be likely that it also affects a randomly chosen patch Y (*Appendix A6*). Here, following Starrfelt & Kokko[3], we represent patches in a lattice connected by dispersal. Colours denote environmental condition on patches at sequential time-points t. See *Appendix A. Wasp: © Z. Soh.*

Figure 2 | Increased stochasticity can increase the potential for selection of altruistic behaviour. Without stochastic effects, altruism evolves when $rb_\mu > c_\mu$ (shown in region '1' in panels **a** and **b** for $c_\mu = 1$, and $r = 0.5$). As stochasticity v rises, the power of $b_\sigma : c_\sigma$ benefits increases, reducing the ratio of $b_\mu : c_\mu$ needed for the evolution of altruism. In **(Panel a)** altruists secure a high $b_\sigma = 0.75$, considerably increasing the scope for altruism (extending region '1' to region '2'). Actors may also reduce the volatility of their personal fecundity (here, $c_\sigma = -0.4$), reducing the magnitude of the total cost C below c_μ and increasing the potential for altruism further (extending to region '3'). Altruism is always deleterious in region '4'. In **(Panel b)**, altruists secure a low $b_\sigma = 0.1$ and personal volatility reduction of $c_\sigma = -0.1$ (regions as in panel **a**). Comparing panel **a** ($b_\sigma = 0.75$) and panel **b** ($b_\sigma = 0.1$), larger reductions of recipient volatility (higher b_σ) result in larger increases in the actor's inclusive fitness. **(Panel c)** The minimum relatedness required for the evolution of altruism under different c_μ values (curved lines, from $c_\mu = 0.05$ to 0.4, when $b_\sigma = 0.75$, $c_\sigma = 0$, and $b_\mu = 0.2$); as stochasticity (v) increases, the minimum required relatedness (r^*) decreases.

Figure 3 | Empirical studies of Hamilton's rule may benefit from incorporating stochasticity. (Panel a) Here, we model sister–sister cooperation between facultatively-social insects: volatility effects can drive the invasion of altruists in regions of parameter space (below the dashed line) in which the means-based Hamilton's rule ($rb_\mu > c_\mu$) is violated. **(Panel b)** These predictions are matched in an individual-based haplodiploid simulation. In both panels **a** and **b**, good and bad years occur equally ($d_\pi = 0.5$) at random. In *Appendix B*, we discuss temporal correlation. Coordinates plot average frequency across five replicate simulations after 1,000 generations, from an initial frequency $p = 0.05$. **(Panel c)** In high-stochasticity conditions, helpers may buffer breeders from profound environmental fluctuations[4,9,11]. We estimate rb_μ values in the Galapagos mockingbird (*Mimus parvulus*), and show that volatility effects can, in principle, drive cooperation (above the dashed line) even when mean fecundity costs c_μ cancel out b_μ (here, $b_\mu = c_\mu = 0.3$). See *Appendix C. Bee: K. Walker (CC-BY 3.0 AU); Mockingbird: BHL (CC-BY 2.0).*

Figure 4 | The trade-off between constitutive and inducible altruism in a stochastic world depends on plasticity costs and information reliability. We show a population fluctuating randomly between a good and a bad environmental state, comprised

of three alleles: 'selfish' (*S*) whose carriers never cooperate; 'constitutive cooperator' (*C*) whose carriers always cooperate; and 'inducible cooperator' (*I*) whose carriers only cooperate when they believe they are in the bad (low-fecundity) state. Information reliability is set by *A* (actors diagnose true state with probability *A*). Apexes represent monomorphic populations. Without social behaviour, individuals obtain 4 and 1 offspring in good and bad states respectively. Cooperation confers on recipients 1.5 additional offspring in bad states but reduces recipient fecundity by 0.2 offspring in good states, and costs actors 0.5 offspring in all states. **(Panel a)** Only considering mean fecundity, the means-based Hamilton's rule $rb_\mu > c_\mu$, commonly used empirically, mistakenly predicts that selfishness (*S*) will dominate. In stochastic conditions cooperation evolves: **(Panel b)** constitutive cooperators invade (to polymorphism) when information is imperfect (*A*=0.75) and there is a plasticity cost (0.1 offspring). **(Panel c)** When information reliability is increased (*A*=1), plastic cooperators outcompete constitutive cooperators. **(Panel d)** However, increasing plasticity costs (here, from 0.1 to 0.3 offspring) eliminates plasticity benefits, allowing constitutive cooperators to invade. Vectors show directions of expected changes in frequencies: these represent continuous expected trajectories when frequencies are constrained to change by small amounts per generation. Relatedness *r*=0.5 in all plots. Details are provided in *Appendix B.*

Extended Data Table E1 | Parameters of the model. For derivation of regression slopes, see *Appendix A.*

Extended Data Figure E1 | The interaction between the frequency of altruists and the effectiveness of altruism. (Panel a) The stochastic Hamilton's rule predicts that selection on volatility-suppressing altruism with fixed costs and benefits can generate negative frequency-dependence and is sensitive to mild mean-fecundity costs (c_μ). We evaluate a population undergoing synchronous fluctuations to identify the frequency *p** at which there is no expected change in allele frequency. We illustrate the result with individual fecundities of 4 and 1 in good and bad years respectively. Relatedness is *r* = 0.5. **(Panel b)** Simulated population outcomes (frequency after 100,000 generations) match predictions of the stochastic Hamilton's rule in panel **a**. Warmer colours denote higher polymorphic frequencies of altruists. In this haploid model (*Appendix B*), 1% of breeding spots are available each year for replacement by offspring that year: with such constraints on the magnitude of the response to selection, radical stochastic shifts in allele frequency over single generations do not occur, allowing the population to settle at equilibria where all alleles have equal expected relative fitness without being continually displaced (*Extended Data* Fig. E3). **(Panel c)** Competing an altruistic allele against a defector allele reveals the action of frequency dependent selection. Here, populations experiencing costs of *c* = 0.2 and *η* = 0.466 converge to *p** = 0.359 from any initial frequency (coloured lines show five starting frequencies from 0.001 to 0.999), as predicted by the stochastic Hamilton's rule.

Extended Data Figure E2 | Stochasticity $v = \frac{(p\eta + (1-p))\sigma_{00}}{\mu_{00} - pc}$ for the model of altruistic bet hedging in *Appendix B* (*Supplementary Information*) plotted against frequency (*p*) and cost (*c*) for three different values of *η* (where lower values of *η* denote greater buffering of recipients from the environment). **(Panels a and b)** When *η* is small, representing high levels of volatility reduction, *v* declines steeply with *p* across the range of costs. When *η* is large **(Panel c)**, the sign of the effect of *p* on *v* depends on *c*. Values of other parameters: z_1 = 4, z_2 = 1, *d* = 0.5.

Extended Data Figure E3 | Weak selection negates the capacity of temporal autocorrelation to drive the frequency of altruistic bet-hedgers away from the convergence frequency. All panels show individual-based simulations from five different initial

frequencies of an altruistic bet hedging allele (p) competing against a non-cooperator. In panel **a**, the population has zero temporal autocorrelation (environmental state in each generation is random). In panel **b**, the population has strong temporal autocorrelation (environmental state in the next generation has a 90% probability of remaining the same as in the current generation). Despite higher amplitude fluctuations, this population converges to the same point (from the five different starting frequencies) as the uncorrelated population (panel **a**). In panel **c**, the same population is simulated with greater gene frequency changes (10% of the resident genotype frequencies are available to change each generation). The population is repeatedly carried to frequencies far from the convergence point. In this case, the utility of the stochastic Hamilton's rule is (*i*) identifying whether a given trait is immune from invasion by competitors and (*ii*) identifying the expected generational change at each frequency p. Parameters are $z_1 = 4$, $z_2 = 1$, $\alpha = 0.5$.