



## Diminishing return of investment in genetic diversity

Bach, Lars; Pertoldi, Cino; Vucetich, John A. ; Loeschcke, Volker; Lundberg, Per

*Published in:*  
Evolutionary Ecology Research

*Publication date:*  
2012

*Document Version*  
Early version, also known as pre-print

[Link to publication from Aalborg University](#)

### *Citation for published version (APA):*

Bach, L., Pertoldi, C., Vucetich, J. A., Loeschcke, V., & Lundberg, P. (2012). Diminishing return of investment in genetic diversity. *Evolutionary Ecology Research*, 14(7), 793-801.

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal -

### **Take down policy**

If you believe that this document breaches copyright please contact us at [vbn@aub.aau.dk](mailto:vbn@aub.aau.dk) providing details, and we will remove access to the work immediately and investigate your claim.

---

## Diminishing return of investment in genetic diversity

Lars A. Bach<sup>1,2,3</sup>, Cino Pertoldi<sup>4,5</sup>, John A. Vucetich<sup>6</sup>,  
Volker Loeschcke<sup>7</sup> and Per Lundberg<sup>2</sup>

<sup>1</sup>The Interacting Minds Centre, Building 1483 3rd, University of Aarhus, Aarhus, Denmark,

<sup>2</sup>Department of Theoretical Ecology, Lund University, Lund, Sweden,

<sup>3</sup>Interdisciplinary Center for Organizational Architecture, Business and Social Sciences,

Aarhus, Denmark, <sup>4</sup>Department 18/Section of Environmental Engineering,

Aalborg University, Aalborg, Denmark, <sup>5</sup>Aalborg Zoo, Aalborg, Denmark,

<sup>6</sup>School of Forest Resources and Environmental Science, Michigan Technological University,  
Houghton, Michigan, USA and <sup>7</sup>Department of Bioscience, Aarhus University, Aarhus, Denmark

---

### ABSTRACT

**Motive:** Priorities in conservation management are often difficult to determine because we lack comparable biodiversity metrics. So that actions can be cost-effective, conservation decision-making and management needs such metrics.

**Question:** What suitable metrics can compare efforts and investments in biodiversity conservation? How can established measures of genetic diversity be combined with the economic return-of-investment paradigm?

**Method:** Use the return-of-investment approach, which has previously been restricted to issues of species diversity. Extend it to include genetic diversity. Use Taylor's power law to relate mean abundance, rates of genetic deterioration, and principles of return-of-investment.

**Key assumptions:** We can specify the relationship between cost of conservation and population size. Time-series data are available for each population. We can approximate the effective population size ( $N_e$ ) of a fluctuating population as the harmonic mean population size.

**Conclusion:** As the financial investment in conservation increases, the estimated marginal increase in genetic diversity diminishes. One can rank actions that increase mean population size according to their associated marginal increases in genetic diversity, thus evaluating which improvements offer the most value for money.

**Keywords:** adaptive potential, biodiversity, conservation, diminishing returns, genetic diversity, return of investment.

### INTRODUCTION

Owing to the wide discrepancy between the means required to safeguard biodiversity and the resources nations and communities are willing to devote to conservation, ways are needed to allocate those resources (Weitzman, 1992; Wilson *et al.*, 2006). To this end, a number of

---

Correspondence: L.A. Bach, The Interacting Minds Centre, University of Aarhus, Jens Chr. Skous Vej 2 Bld. 1483, 8000 Aarhus C, Denmark. E-mail: lbach@cs.au.dk

Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

studies have recently applied the return-of-investment (ROI) approach to conservation resource allocation problems. Recommendations have been made to make any assessments as precise as possible, such as taking account of the precise costs of the conservation efforts (Naidoo *et al.*, 2006; Murdoch *et al.*, 2007; Bode *et al.*, 2008; Carwardine *et al.*, 2008) and the spatial heterogeneity of socioeconomic factors (Chan and Daily, 2008; Polasky *et al.*, 2008). The ROI approach has been shown to be more effective than other methods in improving the efficiency of conservation investment and in ensuring better biodiversity preservation when resources are limited (Ando *et al.*, 1998; Murdoch *et al.*, 2007; Carwardine *et al.*, 2008). Usually, such analyses aim to maximize the number of species or number of endemic species protected, which in turn is based on the species–area relationship (MacArthur and Wilson, 1967). Previously, ROI has focused on (i) conservation from a demographic perspective and (ii) conservation of habitat types. An important yet neglected aspect of conservation is the maintenance of genetic diversity and viability (Schwartz *et al.*, 2007). Here, we expand the approach to accommodate this aspect because the sustainability of species and habitats ultimately depends on genetic viability. Obviously, many natural populations of the same species are interconnected and hence mutually influenced demographically and genetically by adaptive migration and range expansions (Bach *et al.*, 2007; Travis *et al.*, 2010).

By applying the principles of ROI to conservation genetics, we hope to distinguish among population conditions and conservation options to identify those which provide the highest marginal genetic diversity return per unit investment. In other words, we suggest equating ROIs across conservation options, not to maximize ROI *per se*, but to maximize genetic diversity.

To apply the principles of ROI to the conservation of genetic diversity, we use Taylor's law, which relates a population's mean abundance to variability in abundance, and the harmonic mean, which relates variability in abundance to the rate of genetic drift. These relationships represent a useful basis for assessing ROI because of their application to a wide range of taxa and, more generally, because much is known about how populations fluctuate (Pimm, 1992; Arino and Pimm, 1995). Because they are based on such general relationships, the results from our ROI analysis are also of general value. Moreover, the principles on which our analysis is based could be applied to specific cases for which information is available on the abundance–variability relationship.

Although the demographic properties of a population may make it appear viable, long-term viability can be severely compromised by the loss of genetic diversity (Keller and Waller, 2002; Spielman *et al.*, 2004). For this reason, the conservation of biodiversity requires enough genetic diversity to ensure the evolutionary potential necessary for populations living in changing environments. Two aspects of such genetic diversity are the rate of inbreeding and relative strength of genetic drift, which are each directly related to a population's effective population size ( $N_e$ ). The amount of genetic variability present in a population is closely related to  $N_e$  (Frankham, 1996). The notion of  $N_e$  is therefore central to the relationship between ecology and genetics and such ecological characteristics as demography, life history, and social structure, while  $N_e$  in turn determines the speed at which the population loses genetic variability (Goldstein and Pollock, 1997; Vucetich and Waite, 1999). Furthermore, in fluctuating populations  $N_e$  is closely (inversely) related to the risk of extinction, since the temporal harmonic mean population size (HM) is the surrogate measure for  $N_e$  and HM is mainly determined by the minimum population sizes in a certain time interval. Very large fluctuations are typically observed in small mammals and heterotherms, but when fluctuations are measured on a per-generation basis they can be of the same magnitude in

large mammals (Sibly *et al.*, 2007). Since in the main  $N_e$  is determined by the minimum point, and the closer the minimum point is to zero the higher the extinction risk, we argue that  $N_e$  helps to predict extinction risk (Vucetich and Waite, 1999; Pertoldi *et al.*, 2008). Given that the increase in inbreeding level ( $F$ ) is related to  $N_e$ , we can deduce that the minimum point also determines the rate of increase in  $F$  per generation.

The advantage of our assessment of the marginal gain in biodiversity is that it is based on established theory and allows comparative analyses potentially applicable both to single species and to communities. The requirements are basically a number of time series for populations at different mean population size and the cost of maintaining the population at a certain size (typically closely related to the price of land). To our knowledge, no previous study has used the ROI conservation approach in the context of genetic diversity of candidate populations. Our goal here is to introduce the conceptual framework; elsewhere we will deal with its application to case study populations.

## RESULTS

In evolutionary ecology, the magnitude of population fluctuations scales systematically with mean abundance (e.g. Desharnais *et al.*, 2006). For example, for a population experiencing constant per capita environmental variability, the regression of  $\log \sigma^2$  (variance) versus  $\log \bar{\mu}$  (arithmetic mean) gives a line with a slope of 2 and this positive relationship between  $\sigma^2$  and  $\bar{\mu}$  can be described using Taylor's power law (Taylor, 1961),

$$\sigma^2 = K\bar{\mu}^\beta, \quad (1)$$

where  $K$  is a constant and  $\beta$  a scaling coefficient. Larger values of  $\beta$  indicate that the variance increases more rapidly with  $\bar{\mu}$  than expected. Values of  $\beta > 2$  are not exceptional, and it has been suggested that  $\beta$  may lie anywhere in the range of 0.6 to 2.8 for animal populations (Taylor and Woivod, 1982). Taylor and Woivod (1982) estimated  $\beta$  for 97 aphid species; for 31 of these species,  $\beta$  was found to be above 2. Cases of  $\beta$  with values well above 2 were also demonstrated in the models presented by Keeling (2000). Furthermore, Pertoldi *et al.* (2007) suggested that increasing environmental variability raises the value of  $\beta$ , so that in populations where  $\beta$  is initially below 2, an increase in environmental variability can take  $\beta$  above the threshold value of 2.

Using equation (1), Pertoldi *et al.* (2007) demonstrated that the harmonic mean of a population's size is approximated by (Fig. 1)

$$HM = \bar{\mu} - K\bar{\mu}^{\beta-1}. \quad (2)$$

Because HM also estimates  $N_e$  (Wright, 1931), one can use equation (2) to quantify how  $N_e$  increases with  $\bar{\mu}$ .

In addition to loss of variability by random genetic drift, inbreeding (defined by the probability,  $F$ , of two randomly chosen alleles being identical by descent) also reduces genetic diversity in small populations. Specifically,  $F$  increases each generation according to  $\Delta F = 1/2 N_e$ , hence by substituting  $N_e$  with (2) we can express the change in the rate of inbreeding as

$$\Delta F = \frac{1}{2(\bar{\mu} - K\bar{\mu}^{\beta-1})}. \quad (3)$$

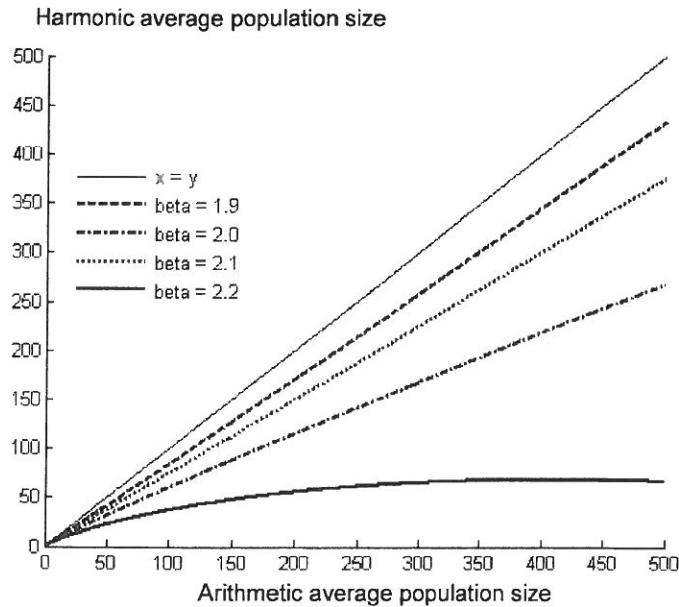


Fig. 1. Numerical examples of equation (2) showing how the harmonic average relates to the arithmetic average for various values of  $\beta$  (with  $K = 0.25$ ).

Figure 2 illustrates how the rate of inbreeding decreases as a function of the arithmetic mean population size.

As noted by Pertoldi *et al.* (2007), the first derivative of equation (2) with respect to  $\bar{\mu}$ ,

$$\frac{\partial \text{HM}}{\partial \bar{\mu}} = 1 - K(\beta - 1)\bar{\mu}^{(\beta-2)}, \quad (4)$$

describes where the trajectory of the HM as a function of  $\bar{\mu}$  inflects from positive to negative. In the context of ROI, this means that we can identify putative domains of negative returns of investment in increasing the mean population size. As shown in Figs. 3a and 3b, the ROI can follow qualitatively different scenarios of return patterns. Such knowledge is important for managers when choosing which populations conservation efforts should be directed at.

Our objective is to characterize how benefits, in the form of enriched genetic diversity, result from investment in larger average population sizes. It is useful to focus on the largest possible marginal return. Let  $\Delta g$  define the (positive) change in genetic diversity resulting from the combination of forces acting at a given arithmetic mean population size. We can then express the goal of maximizing the marginal gain as

$$\max(\Delta g_{i,j} / \Delta \cos t_{i,j}) \quad (5)$$

where  $\Delta g_{i,j}$  is the change in genetic diversity of species  $i$  in population  $j$  and  $\Delta \cos t_{i,j}$  is the corresponding conservation investment.

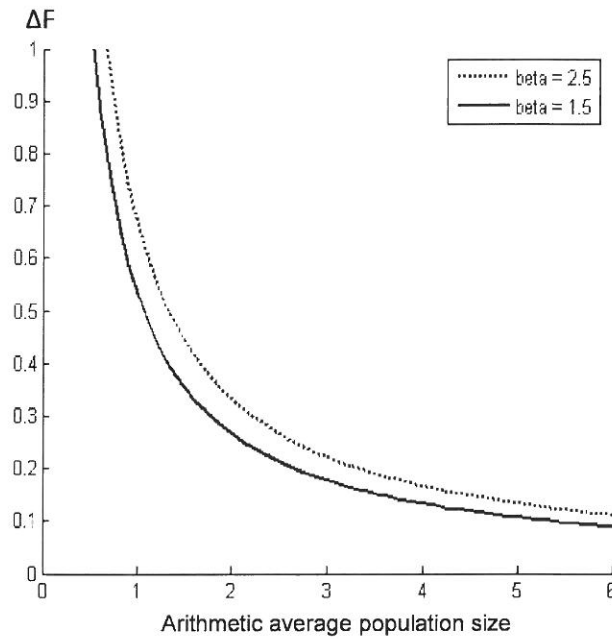


Fig. 2.  $\Delta F$  as a function of arithmetic average population size with  $K = 0.25$  and  $\beta = 1.5$  or  $2.5$ .

If we suppose that the cost of a protected area is linearly related to the mean population size, we have

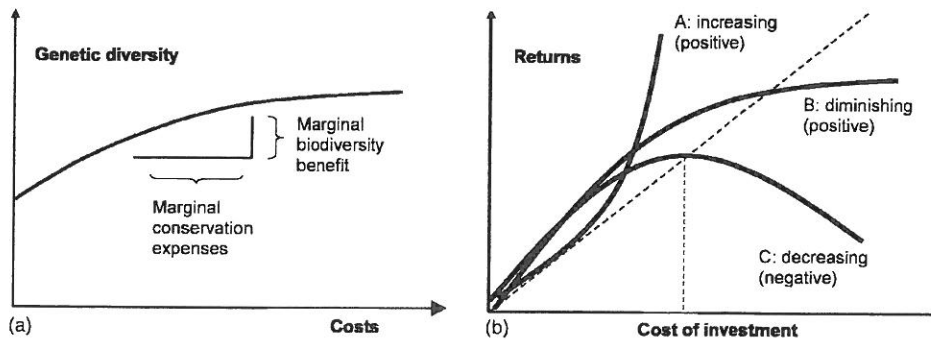
$$\max(\Delta g / \Delta \cos t) = \max(\partial \text{HM} / \partial \bar{\mu}) = \max(1 - K(\beta - 1)\bar{\mu}^{(\beta - 2)}). \tag{6}$$

For non-negative values of  $\bar{\mu}$ , and for all values of  $K$  and  $\beta < 1$ , the maximum value for the rightmost expression in equation (6) is  $\bar{\mu} = 0$ . This means that when maximizing the ratio of gain to cost based on equation (5), the population is zero and no land has been conserved. Clearly, this demonstrates that the marginal gain *per se* should not be the focus of the analysis, but rather used for the purpose of comparison. These properties of equation (6) are not unique to applications of ROI to genetic aspects of conservation. They apply to any circumstances in which the benefit to conservation (in this case,  $g$ ) increases as a decelerating function of *cost*.

### DISCUSSION

Preservation of species diversity is important and the irreversibility of losing species remains a challenge. For a given species, priorities may have to be set between different populations from different locations and here our proposed approach could play a role in ensuring the greatest estimated gain in genetic diversity.

There are, however, several other complications associated with the preservation of biodiversity and/or genetic variability. A long-standing debate in ecology is concerned with the effect of diversity on the temporal stability of biological systems. The ecological consequences of biodiversity loss have received increasing attention over the past decade



**Fig. 3.** (a) Marginal genetic diversity return of investment, where the cost is related to the price of land area assumed to map directly onto the number of individuals. Cost can be defined as (number of individuals/area) times the cost of area, thus including heterogeneity in the quality/cost ratio. (b) The qualitative differences among the returns scenarios. Note that the vertical dashed line corresponds to equation (4) being zero.

(Bangert *et al.*, 2005; Reusch *et al.*, 2005). Current theory suggests that diversity has contrasting effects on the temporal stability of populations and communities (Tilman, 1996). Theoretical work suggests a paradoxical effect of diversity on the temporal stability of ecological systems: increasing diversity should result in decreased stability of populations, whereas community stability is enhanced (Tilman, 1996). While empirical work corroborates that community stability tends to increase with diversity, investigations of the effect of diversity on populations have not revealed any clear patterns. This consideration, together with the observation that changes in vital rate may have opposing effects on growth rate and  $N_e$ , is important as it can produce disagreement about optimal management strategies. It is well known that demographic instability in a population is translated into fluctuations of  $N$  and a reduced  $N_e$  that is close to the harmonic mean of the varying  $N$  values (Vucetich *et al.*, 1997). Therefore, a management strategy with the goal of preserving biodiversity at the community level could theoretically lead to a reduction of  $N_e$  in single populations. In the same way, the attempt to increase growth rate in a population by modifying some of the vital rates can also result in a reduction of  $N_e$ . An increase in growth rate will increase  $N$  and therefore reduce the demographic stochasticity that is related to the population risk of extinction, but may simultaneously lead to a reduction of the genetic diversity due to stronger fluctuations.

An additional complication derives from the fact that the advantage of having genetic variability stems from considering short- and long-term adaptability and evolution in a changing environment. However, this is not universally true; for example, in a constant environment genetic variability in a quantitative character creates a segregational load each generation due to stabilizing selection against individuals that deviate from the optimum phenotype (Lande and Shannon, 1996). Consider a presumably common situation where natural selection acting on quantitative characters favours intermediate phenotypes. In an intermediate-optimum model, the genetic variability may be either beneficial or detrimental, depending on the pattern of environmental change (the frequency, the amplitude, and the degree of autocorrelation of the environmental oscillations) (Lande and Shannon, 1996; Ranta *et al.*, 2008; Björklund *et al.*, 2009, 2011).

In spite of complicating issues, we believe that this method in combination with other economic metrics of preservation efforts can provide a useful approach to managers and decision-makers for comparisons between populations and the subsequent setting of priorities on an informed basis. In addition, the above demonstration of problems by focusing exclusively on maximizing marginal gain is valuable because one goal for the field of ecological economics is to understand which principles of conventional economics will need to be revised and which are appropriate for societies committed to conservation.

Another benefit of this description of population dynamics and genetic diversity is that potentially it would be possible to suggest whether two (semi)-separate populations or one single larger population provides the most conservation value for money. This kind of question has been referred to as the SLOSS debate (see Higgs and Usher, 1980; Simberloff, 1988). Given the diminishing returns relation observed above, we can conclude that expenditures give the highest 'genetic' payoff when distributed among several small populations, *ceteris paribus*. Although our proposed analysis only requires population size data, the use of ROI to guide the conservation of genetic diversity could be developed towards more specific analyses. If available, it may be constructive to include detailed genetic information of the populations in question such as, for example, the genetic diversity associated with QTL markers for ecologically relevant traits. It should be stressed, however, that molecular markers may be very species specific and even population specific, which means that variation in the abundance–variability relationship may bias analyses in terms of comparisons.

Expecting to find the perfect unambiguous prioritization tool is bound to fail; however, we wish to stress the point that from population data sets we can obtain an indication of the actual gain (loss) of expanding (lowering) the mean population size. This will allow a comparison of conservation scenarios in order to determine the best return of investment providing (biodiversity) value for (conservation) money. To our knowledge, no attempt has been made to implement the concept of  $N_e$  and genetic diversity measures in the ROI conservation tools developed to date.

#### ACKNOWLEDGEMENTS

We wish to thank the anonymous reviewers and Hugh P. Possingham for valuable suggestions on an earlier version of the manuscript. This research project was supported by Ecoclim, a Nordic Council of Ministers centre of excellence. We thank the Danish Natural Science Research Council for financial support to C.P. (grants #11-103926, #09-065999, and #95095995) as well as the Carlsberg Foundation (grant #2011-01-0059). J.A.V. was supported by the US National Science Foundation (DEB-9903671).

#### REFERENCES

- Ando, A., Camm, J., Polasky, S. and Solow, A. 1998. Species distribution, land values, and efficient conservation. *Science*, **279**: 2126–2128.
- Arino, A. and Pimm, S.L. 1995. On the nature of population extremes. *Evol. Ecol.*, **9**: 429–443.
- Bach, L.A., Ripa, J. and Lundberg, P. 2007. On the evolution of conditional dispersal under environmental and demographic stochasticity. *Evol. Ecol. Res.*, **9**: 663–673.
- Bangert, R., Turek, R.J., Martinsen, G.D., Wimp, G.M., Bailey, J.K. and Whitham, T.G. 2005. Benefits of conservation of plant genetic diversity to arthropod diversity. *Conserv. Biol.*, **19**: 379–390.

- Björklund, M., Ranta, E., Kaitala, V., Bach, L.A., Lundberg, P. and Stenseth, N.C. 2009. Quantitative trait evolution and environmental change. *PLoS One*, **4**(2): e4521.
- Björklund, M., Ranta, E., Kaitala, V., Bach, L.A. and Lundberg, P. 2011. Environmental fluctuations and level of density-compensation strongly affects the probability of fixation and fixation times. *Bull. Math. Biol.*, **73**: 1666–1681.
- Bode, M., Wilson, K.A., Brooks, T.M., Turner, W.R., Mittermeier, R.A., McBride, M.F. *et al.* 2008. Cost-effective global conservation spending is robust to taxonomic group. *Proc. Natl. Acad. Sci. USA*, **105**: 6498–6501.
- Carwardine, J., Wilson, K.A., Watts, M., Etter, A., Klein, C.J. and Possingham, H.P. 2008. Avoiding costly conservation mistakes: the importance of defining actions and costs in spatial priority setting. *PLoS One*, **3**(7): e2586.
- Chan, K.M.A. and Daily, G.C. 2008. The payoff of conservation investments in tropical countryside. *Proc. Natl. Acad. Sci. USA*, **105**: 19342–19347.
- Desharnais, R.A., Costantino, R.F., Cushing, J.M., Henson, S.M., Dennis, B. and King, A.A. 2006. Experimental support of the scaling rule for demographic stochasticity. *Ecol. Lett.*, **9**: 537–547.
- Frankham, R. 1996. Relationship of genetic variation to population size in wild-life. *Conserv. Biol.*, **10**: 1500–1508.
- Goldstein, D.B. and Pollock, D.D. 1997. Launching microsatellites: a review of mutation processes and methods of phylogenetic inference. *J. Hered.*, **88**: 335–342.
- Higgs, A.J. and Usher, M.B. 1980. Should nature reserves be large or small. *Nature*, **285**: 568–569.
- Keeling, M.J. 2000. Simple stochastic models and their power-law type behaviour. *Theor. Pop. Biol.*, **58**: 21–31.
- Keller, L.F. and Waller, D.M. 2002. Inbreeding effects in wild populations. *Trends Ecol. Evol.*, **17**: 230–241.
- Lande, R. and Shannon, S. 1996. The role of genetic variation in adaptation and population persistence in changing environments. *Evolution*, **50**: 434–437.
- MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Murdoch, W.W., Polasky, S., Wilson, K.A., Possingham, H.P., Kareiva, P. and Shaw, R. 2007. Maximising return on investment in conservation. *Biol. Conserv.*, **139**: 375–388.
- Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H. and Rouget, M. 2006. Integrating economic costs into conservation planning. *Trends Ecol. Evol.*, **21**: 681–687.
- Pertoldi, C., Bach, L.A., Barker, J.S.F., Lundberg, P. and Loeschcke, V. 2007. The consequences of the variance–mean rescaling effect on effective population size. *Oikos*, **116**: 769–774.
- Pertoldi, C., Bach, L.A. and Loeschcke, V. 2008. On the brink between extinction and persistence. *Biol. Direct.*, **3**: 47.
- Pimm, S.L. 1992. *The Balance of Nature?* Chicago, IL: University of Chicago Press.
- Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E. *et al.* 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol. Conserv.*, **141**: 1505–1524.
- Ranta, E., Kaitala, V., Björklund, M., Lundberg, P., Bach, L.A. and Stenseth, N.C. 2008. Environmental forcing and genetic differentiation in subdivided populations. *Evol. Ecol. Res.*, **10**: 1–9.
- Reusch, T.B.H., Ehlers, A., Hämmerli, A. and Worm, B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci. USA*, **102**: 2826–2831.
- Schwartz, M.K., Luikart, G. and Waples, R.S. 2007. Genetic monitoring: a promising tool for conservation and management. *Trends Ecol. Evol.*, **22**: 25–33.
- Sibly, R.M., Barker, D., Hone, J. and Page, M. 2007. On the stability of populations of mammals, birds, fish and insects. *Ecol. Lett.*, **10**: 970–976.

- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.*, **19**: 473–511.
- Spielman, D., Brook, B.W. and Frankham, R. 2004. Most species are not driven to extinction before genetic factors impact them. *Proc. Natl. Acad. Sci. USA*, **101**: 15261–15264.
- Taylor, L.R. 1961. Aggregation, variance and the mean. *Nature*, **189**: 732–735.
- Taylor, L.R. and Woiwod, I.P. 1982. Comparative synoptic dynamics. 1. Relationships between inter- and intra-specific spatial and temporal variance mean population parameters. *J. Anim. Ecol.*, **51**: 879–906.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology*, **77**: 350–363.
- Travis, J.M.J., Münkemüller, T. and Burton, O.J. 2010. Mutation surfing and the evolution of dispersal during range expansions. *J. Evol. Biol.*, **23**: 2656–2667.
- Vucetich, J.A. and Waite, T.A. 1999. Erosion of heterozygosity in fluctuating populations. *Conserv. Biol.*, **13**: 860–868.
- Vucetich, J.A., Waite, T.A. and Nunney, L. 1997. Fluctuating population size and the ratio of effective to census population size. *Evolution*, **51**: 2017–2021.
- Weitzman, M. 1992. On diversity. *Q. J. Economics*, **107**: 363–406.
- Wilson, K.A., McBride, M., Bode, M. and Possingham, H.P. 2006. Prioritising global conservation efforts. *Nature*, **40**: 337–340.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics*, **16**: 97–159.