



Reply to Wootton and Pfister: The search for general context should include synthesis with laboratory model systems

Wootton and Pfister (1) note the striking contrast between the results of their elegant field study (2) and our laboratory study (3), both of which manipulated genetic diversity and population size independently. Wootton and Pfister (1) found that population size most strongly influences extinction risk, whereas we (3) found that genetic diversity matters as much as population size in reducing extinction, and that genetic diversity also increases long-term growth rates of extant populations. Given the implications for management of small populations, it is crucial to understand why our results differ.

Wootton and Pfister (1) propose that environmental variability present in the field may be key to the difference in outcome. We agree that high environmental variability could increase the importance of founding population size relative to genetic diversity, particularly for species like the sea palm (2), where environmentally driven Allee effects are strong. We disagree fundamentally, however, with the notion that it is only possible to observe an effect of environmental stochasticity in nature. To the contrary, in the laboratory, environmental variability can be manipulated experimentally with sufficient replication, making it possible to examine exactly how it operates and its relative importance.

Another difference in our experiments that could explain our different results is the timing of treatments: implementing them upon founding (2) versus later as a rescue treatment (3). We previously conducted a founder effect experiment similar to that in the Wootton and Pfister study (2), and in our study (4), establishment was strongly driven by number of founders, not their genetic background. Thus, the timing of the manipulation of diversity and numbers can play a role and should be explored further.

We agree with Wootton and Pfister (1) that the sudden environmental change our study imposed (as with reintroduction of a species to the wild or a disturbance such as deforestation) might lead to different results than a more gradual environmental shift (as with ocean acidification or accumulation of pollutants). Genetic diversity should be more important for establishment under novel selection. The difference in extinction risk between abruptly and gradually changing environments can be studied explicitly with laboratory systems and mathematical models as well as through synthesis with field systems.

Wootton and Pfister's final point is that the dominant processes driving extinction might be species-specific (1). To some degree that must be true. By examining important intrinsic and extrinsic commonalities and differences between systems, explicit hypotheses can be formulated and tested rigorously, thus providing generality. For example, haplodiploid species like sea palm should be less likely to accumulate deleterious mutations (2), and thus low genetic diversity may reduce fitness less than in diploid species, like the *Tribolium* model system. This biological hypothesis can be tested in other systems and through careful laboratory experiments.

Thus, we agree that differences in results underscore the importance of additional research, but disagree that the research should focus on populations in the field. By synthesizing results across laboratory and field studies, ideally with open data, we have the best chance of providing effective, evidence-based management of biological diversity (5).

ACKNOWLEDGMENTS. Funding for this research was provided by the US National Science Foundation [Grant

DEB-0949619, Grant DEB-0949595, Graduate Research Fellowship DGE-1321845 Amend. 3 (to M.J.K.), and two associated Research Experiences for Undergraduates supplements], and additional support came from the US Department of Agriculture via the Colorado Agricultural Experiment Station.

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1 Wootton JT, Pfister CA (2015) Processes affecting extinction risk in the laboratory and in nature. *Proc Natl Acad Sci USA*, 10.1073/pnas.1516561112.

2 Wootton JT, Pfister CA (2013) Experimental separation of genetic and demographic factors on extinction risk in wild populations. *Ecology* 94(10):2117–2123.

3 Hufbauer RA, et al. (2015) Three types of rescue can avert extinction in a changing environment. *Proc Natl Acad Sci USA* 112(33):10557–10562.

4 Szűcs M, Melbourne BA, Tuff T, Hufbauer RA (2014) The roles of demography and genetics in the early stages of colonization. *Proc Biol Sci* 281(1792):20141073.

5 Gomulkiewicz R, Shaw RG (2013) Evolutionary rescue beyond the models. *Philos Trans R Soc Lond B Biol Sci* 368(1610):20120093.

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The authors declare no conflict of interest.

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