

Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming

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Populations of many species are dramatically declining worldwide, but the causal mechanism remains debated among different human-related threats. Coping with this uncertainty is critical to several issues about the conservation and future of biodiversity, but remains challenging due to difficulties associated with the experimental manipulation and/or isolation of the effects of such threats under field conditions. Using controlled microcosm populations, we quantified the individual and combined effects of environmental warming, overexploitation and habitat fragmentation on population persistence. Individually, each of these threats produced similar and significant population declines, which were accelerated to different degrees depending upon particular interactions. The interaction between habitat fragmentation and harvesting generated an additive decline in population size. However, both of these threats reduced population resistance causing synergistic declines in populations also facing environmental warming. Declines in population size were up to 50 times faster when all threats acted together. These results indicate that species may be facing risks of extinction higher than those anticipated from single threat analyses and suggest that all threats should be mitigated simultaneously, if current biodiversity declines are to be reversed.

Keywords: species; population persistence; extinction risk; human-caused threats; climate change; overfishing

1. INTRODUCTION

Increase in the loss of species due to human-related threats is a major concern in modern ecology and conservation (Myers 1995; Pimm *et al.* 1996; Chapin *et al.* 2000; Pimm & Rave 2000; Sala *et al.* 2000; Novacek & Cleland 2001; Jenkins 2003). The decline of wild populations, which leads to species extinctions and consequently to reductions in overall biodiversity, has been mainly attributed to the effects of habitat fragmentation, over-exploitation and global warming (see reviews by Myers 1995; Chapin *et al.* 2000; Sala *et al.* 2000; Novacek & Cleland 2001; Jenkins 2003; Parmesan & Yohe 2003). The specific effects and interactions of these threats remain, however, controversial because all threats do provide rational mechanisms to explain population declines; threats usually occur simultaneously and as yet there has been a lack of robust studies fully isolating their individual and combined effects (e.g. Myers 1995; Novacek & Cleland 2001; Jenkins 2003; Schiermeier 2003; Aronson *et al.* 2004; Buckley & Roughgarden 2004; Worm & Myers 2004; Grigg *et al.* 2005). Such uncertainty is regarded as one of the most important challenges in modern ecology (Myers 1995; Chapin *et al.* 2000; Sala *et al.* 2000; Novacek & Cleland 2001) and it is a major limitation in the construction of future projections on biodiversity change (Myers 1995; Sala *et al.* 2000),

generation of effective conservation strategies (Schiermeier 2003; Worm & Myers 2004; Grigg *et al.* 2005) and quantification of extinction risks (Myers 1995; Sala *et al.* 2000; Novacek & Cleland 2001).

The potential mechanisms by which these threats are likely to affect species are relatively well acknowledged. Habitat fragmentation, for instance, increases the distance between populated habitats, which, in turn, reduces population connectivity and replenishment through immigration (Hanski 1998; Debinski & Holt 2000). The inflow of immigrants directly influences population dynamics and by introducing new genotypes it increases resistance and the speed of recovery (i.e. resilience) following perturbations. The inflow of immigrants also reduces the effects of inbreeding depletion, expands the geographical ranges of species, sustains populations that could not be maintained through self-recruitment and affects the probability of stochastic local extinctions (Hanski 1998; Debinski & Holt 2000; Cloberg *et al.* 2001; Mora & Sale 2002). In contrast, overexploitation removes members from the stock population beyond natural levels of replenishment causing populations to decline and indirectly reducing genetic diversity and the ability to adapt to other threats (Botsford *et al.* 1997; Jackson *et al.* 2001; Myers & Worn 2002; Pauly *et al.* 2002, 2003). Likewise, global warming is likely to reduce population size by causing mortality of non-resistant genotypes or by upsetting thermo-sensitive processes, such as reproduction (O'Brien *et al.* 2000; Mora & Ospina 2001, 2002; Stenseth 2002; Walther *et al.* 2002;

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Parmesan & Yohe 2003). Alternatively, population density could be reduced to balance the higher energetic demands of maintaining metabolism in warmed environments (Poertner *et al.* 2001; Allen *et al.* 2002). Warming is also likely to displace optimum habitats, which may or may not be colonized depending upon species' capabilities to migrate (Warren *et al.* 2001). In the marine realm, warming is also likely to affect other environmental variables, such as rainfall and salinity, marine currents and productivity, all of which may affect populations in different ways and certainly complicates identifying the mechanism that causes populations to change under warming regimes. Unfortunately, while rational explanations exist for the mechanisms by which habitat fragmentation, overexploitation and warming affect biodiversity, identifying their actual effects in natural conditions has been challenging, because field experiments (to quantify and isolate their effects) are constrained by the spatial scales at which these threats operate and because, in most cases, these threats are occurring simultaneously.

A promising approach to reveal the causal link between environmental threats and biodiversity change is the use of microcosm experiments. Microcosms reduce ecosystem complexity allowing the isolation and test of specific factors (Huston 1999; Jessup *et al.* 2004). They also minimize confounding factors that plague observational studies, allow high degree of experimental control, replication and accuracy, and using organisms with short generations, they provide relatively fast results even about processes that could be impossible to measure in nature during the span of a human life (Jessup *et al.* 2004). Microcosms have been useful in the understanding of many functional relationships that include environmental variables, fluctuating environments, ecological interactions, life-history traits, population dynamics, biodiversity, ecosystem functioning and evolution (e.g. Gause 1934; Hairston *et al.* 1968; Davies *et al.* 1998; McGrady-Steed *et al.* 1998; Petchey *et al.* 1999; Kassen *et al.* 2000; Fukami & Morin 2003; Fryxell *et al.* 2005; Kussell & Leibler 2005; Smith *et al.* 2005, reviewed by Jessup *et al.* 2004). On the downside, however, microcosms minimize ecosystem complexity and the multidimensionality of natural conditions. This characteristic has curiously been argued as the strength (Drenner & Mazumber 1999; Huston 1999; Jessup *et al.* 2004) and weakness (Carpenter 1999) of microcosms and of the entire field of experimental ecology (Huston 1999). However, reviews on the topic (i.e. Huston 1999; Jessup *et al.* 2004) have suggested that microcosms are a necessary step towards the understanding of complex ecological processes. Field experiments to assess factors, such as for instance the effect of harvesting, habitat fragmentation and warming at the scale that these occur are simply not feasible because the number of other environmental factors and variety of species is so great that an 'empirical model of (such system) is both conceptually and logistically intractable' (Huston 1999). The characteristics of microcosms and their broad use support their importance for revealing the causal link between human threats and biodiversity decline, particularly, when other approaches are scarce and when the current loss of biodiversity urgently calls for answers to mitigate deterring factors. Here, we used

this tool to quantify the individual and combined effects of habitat fragmentation, overexploitation and environmental warming on population persistence.

2. MATERIAL AND METHODS

(a) *Study species*

We used the rotifer species, *Brachionus plicatilis*, as the subject for this study. This species was chosen because it is easy to culture in captivity, its populations can stabilize at constant conditions (King 1967) and without expensive equipment cultures remain free of contamination. Contamination can be a problem with smaller organisms and may introduce confounding factors. This species is also highly prolific and can alternate reproductive strategies, which maximize its recovery from reductions in population size and enhance its levels of adaptation to selective forces (e.g. Yoshida *et al.* 2003). This suggests that the population responses of such organisms, to the factors analysed, are a very conservative measure of the potential effect that these factors may have on less resilient species.

(b) *Experimental populations*

We first generated a stock supply of the rotifer species. The stock was kept in three 20 l containers, which were placed in a room at 25°C and 12 h light cycle. The stock was fed approximately every 12 h with a constant supply of approximately 230 000 cells of *Nannochloropsis* sp. (Instant Algae) per millilitre of stock. This led to a constant population size of 60 rotifers per millilitre after two weeks, which was maintained throughout the experiment. Four weeks after the stock was set-up, two of the stock containers were mixed and used to fill 300 transparent 50 ml centrifuge vials, which became the experimental microcosm populations. Throughout the experiment, microcosms and the remaining stock container were fed with the same food ratio and kept under the same light cycle. Vials and stock containers were constantly aerated and approximately 50% of their water was replaced every other day. To minimize the risk of contamination, the water used was filtered with a 1 µm filter and irradiated with UV light.

(c) *Experimental design*

Our factorial experiment consisted of 300 replicate microcosm populations, initially at equilibrium, which were exposed to the effects of warming, harvesting and reductions in the input immigrants (see scheme in figure 1). We used reductions in immigration as our surrogate for increases in habitat fragmentation. Our rationale is that habitat fragmentation increases isolation among populated patches, thereby reducing the amount of immigrants replenishing local populations (after Hanski 1998). It is important to clarify that, here, we are only dealing with the effect of the isolation produced by habitat fragmentation. Habitat fragmentation results from habitat loss, which may reduce the size of local populations if habitable area influences carrying capacity. This latter effect was not considered in the present study to avoid increases in the complexity of the experiment and risks of contamination associated with large experiments. Note that adding one more treatment with five levels to this experiment would have increased our number of microcosms to 1500. In this experiment, we considered as controls the populations that were exposed to no warming, no harvesting and had the highest inputs of immigrants.

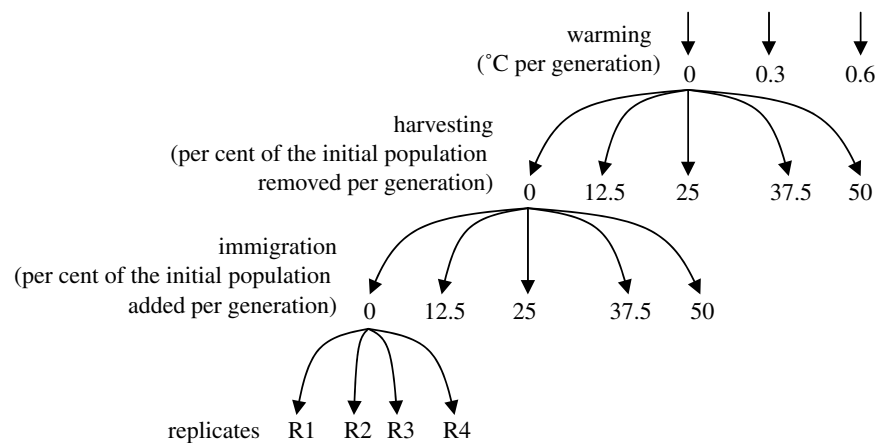


Figure 1. Diagram of the experimental design. The experiment consisted of three treatments for warming, five treatments for harvesting and five treatments for immigration; each treatment with four replicate microcosm populations (300 microcosm populations were deployed in total). For display purposes, arrows are shown to depict one treatment for each threat.

The highest level of immigration was chosen as the control for habitat fragmentation, because the opposite was to use total deprivation of immigration, which is the actual effect of this simulated threat.

All microcosm populations (i.e. vials) were submerged into larger transparent aquaria to allow better control of water temperature (i.e. 12 aquaria, each with 25 vials). Each aquarium was equipped with an electronic temperature control (Autonics TZ4S), a temperature sensor (Autonics PT100) and two 300 W heaters. Using this set-up, water temperature was controlled with 0.1°C accuracy. Each of the microcosm populations, in each of the 12 aquaria, was exposed to one of the five levels of harvesting and immigration ranging from 0 to 50% removal or addition of the individuals in the initial population (figure 1). The maximum levels of harvesting and immigration were chosen based on reports about the levels of current exploitation and immigration to wild populations. Four aquaria were maintained at a constant temperature (i.e. 25°C), whereas the other eight were warmed to 33°C at a gradual rate of either 1 or 2°C per week. Note that standardized to the generation time of this rotifer species, these rates are equivalent to about 0.3 or 0.6°C per generation. These heating rates scale reasonably with warming rates that long-lived organisms might experience, considering that global average temperatures may increase from 1.4 to 5.8°C over the next century (Houghton *et al.* 2001) and that regional variation can be more intense due to localized thermal phenomena, such as El Niño (Fedorov & Philander 2000). The individuals used to replenish the microcosm populations (i.e. for the immigration treatment) were obtained from the stock. These individuals were added directly to populations at constant temperatures or slowly warmed to the temperature of warming treatments to avoid mortality due to thermal shock. In total, four replicated microcosm populations were used for each level of harvesting, immigration and warming. Densities of the microcosm populations were measured when warmed aquaria reached 33°C and after eight weeks in the aquaria that were kept at constant temperature.

(d) Data analysis

Change in population density for each microcosm population was calculated proportional to the initial density and standardized to generation time as $((\text{final density} - \text{initial density}) / \text{initial density}) / \text{number of rotifer generations}$. In the

Q4 analysed species generation days (unpublished data). Changes in population time averaged 2.06 density among the different treatments were analysed with a factorial generalized linear model.

3. RESULTS

(a) Independent effect of threats

We found that independently all simulated threats caused significant population declines ($p < 0.000001$; figure 2; table 1 in the electronic supplementary material). In contrast to control populations (i.e. populations with no warming, no harvesting and were replenished with immigrants), which changed only -1.4% per generation (± 15 s.d.; figure 2; table 2 in the electronic supplementary material), all harvested populations declined below this value reaching a maximum decline of -13.4% per generation (± 6 s.d.) at 50% harvesting per generation (figure 2; table 2 in the electronic supplementary material). The fact that a 50% population harvest per generation led to only a 13.4% decline in population size per generation indicates the fast population turnover in this rotifer species. In absolute terms, however, such a decline was 9.6 times faster than the change observed among non-harvested populations.

Reductions in immigration showed negative effects on population size, when immigration was below 25% input per generation, reaching a maximum population decline of -16.6% per generation (± 16.9 s.d.) when populations were totally deprived from immigration (figure 2; table 2 in the electronic supplementary material). This was a rate of decline 11.9 times faster than the change among replenished control populations (figure 2; table 2 in the electronic supplementary material). The fact that levels of immigration above 25% per generation did not cause burst increases in population density most probably reflects density-dependent control of population size and the stabilization of populations at carrying capacity.

Under control conditions of harvesting and immigration, both heating rates produced similar population declines (figure 2). This is an interesting result because one would have expected larger population declines at the quicker heating rate. However, it is important to note that the control conditions of this experiment included high inputs of immigrants. It is therefore most probable that the individuals counted in the treatments at both heating rates

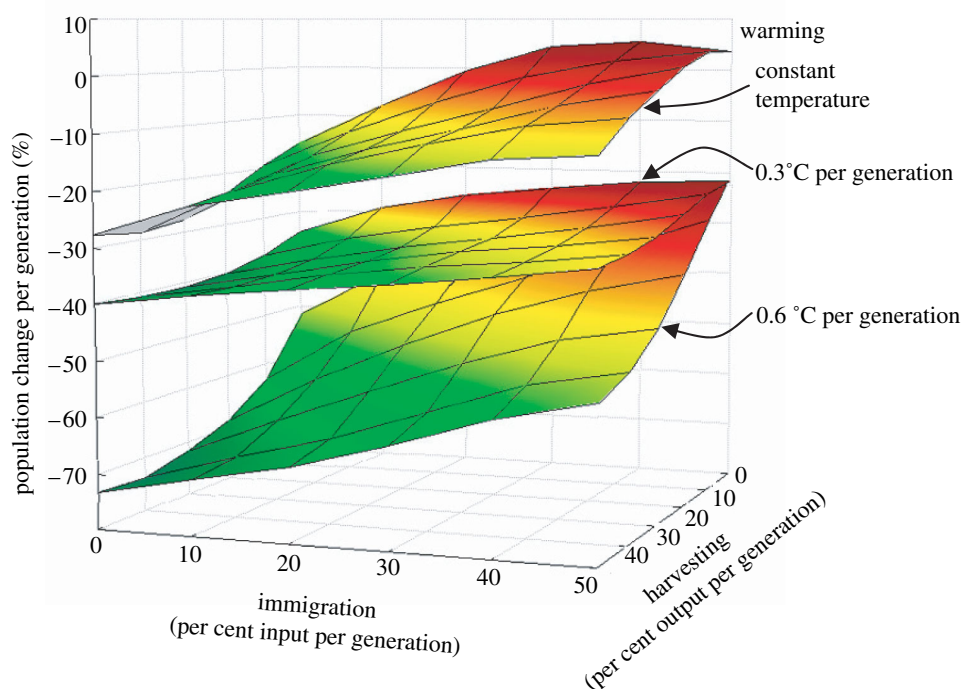


Figure 2. Changes in population density, per generation, of populations exposed to harvesting and reductions in immigration, when facing constant and warming temperatures. The contours in the graph were based on averages of four replicated microcosms for each interaction of treatments. The raw data of this figure appear in table 2 in the electronic supplementary material.

were immigrants. This ‘artefact’ has previously been observed in microcosm experiments and has been used to point the existence of sink populations (i.e. populations located in areas of extreme conditions, where self-replenishment is low to none and populations are maintained almost solely by immigration; e.g. Davies *et al.* 1998). When populations were deprived of immigration, population size at the quick heating rate declined 1.4 times faster than populations facing slower environmental warming (figure 2; table 2 in the electronic supplementary material). Fast warming caused population declines of -17.5% (± 8 s.d.) per generation or a decline 11.8 times faster than control non-warmed populations.

(b) Pairwise effect of threats

The interaction between immigration and warming was significant ($p < 0.004$; table 1 in the electronic supplementary material). Although all populations showed negative growths when facing warming (figure 2), deprivation of immigration accelerated such declines up to -50.8% (± 20 s.d.) per generation under fast warming. This decline was 36.2 times faster than the change observed among control populations (figure 2; table 2 in the electronic supplementary material). Harvesting also showed a significant interaction with warming ($p < 0.05$; table 1 in the electronic supplementary material). Population declines were accelerated up to -51.3% (± 12.9 s.d.) per generation, when populations experienced high levels of harvesting and fast warming. This was a decline 36.6 times faster than the change observed among control non-harvested populations at constant temperatures (figure 2; table 2 in the electronic supplementary material). In general, rapid warming synergized the negative effects of harvesting and immigration deprivation (compare population declines at slow and fast warming rates in figure 2).

Finally, the interaction between harvesting and immigration was non-significant ($p = 0.71$). Populations that were intensely harvested and also deprived from immigration, in control conditions (i.e. no warming), declined -25.7% (± 7.5 s.d.) or 18.5 times faster than control non-harvested and replenished populations (figure 2; table 2 in the electronic supplementary material). This net decline was about the same as adding the independent effect of both threats.

(c) Effect of all threats combined

The interaction among harvesting, immigration and warming was non-significant ($p = 0.19$; table 1 in the electronic supplementary material). Although this third-order interaction did not cause accelerated declines in population size, the net effect of all the three factors acting together led to the largest declines in population size observed in this experiment (figure 2). Populations that were harvested and deprived from immigration and were in fast-warming environments declined -71.7% per generation (± 11.7 s.d.) or a decline 51.6 times faster than control non-harvested and replenished populations at constant temperatures (figure 2).

4. DISCUSSION

Increases in the rate of harvesting of wild species, destruction of their habitats and warming of their environment poses a major threat on their persistence (Myers 1995; Chapin *et al.* 2000; Sala *et al.* 2000; Jackson *et al.* 2001; Novacek & Cleland 2001; Jenkins 2003; Parmesan & Yohe 2003). The simultaneous occurrence of such threats has generated a major challenge to unravel their independent and combined effects through field experimentation, which, in turn, has generated uncertainty and strong controversies, but

513 more importantly has precluded the development of
 514 earnest mitigation policies (e.g. Myers 1995; Novacek &
 515 Cleland 2001; Jenkins 2003; Schiermeier 2003;
 516 Aronson *et al.* 2004; Buckley & Roughgarden 2004;
 517 Worm & Myers 2004; Grigg *et al.* 2005). Using a
 518 microcosm experiment (see §1 for general description
 519 of pros and cons), we showed that independently each
 520 of these threats caused similar and significant popula-
 521 tion decays. As we mentioned in §1, different
 522 Q5 mechanisms can be involved in such declines. In threats
 523 that cause direct mortality, such as harvesting and
 524 warming, the natality may not even up the mortality
 525 losses, thereby leading to negative population growths.
 526 Other mechanisms may involve the effects of drift or
 527 perhaps depensation (i.e. reductions in *per capita*
 528 reproductive success at low population levels; e.g.
 529 Q6 Myers *et al.* 1995) in small depleted populations,
 530 inbreeding depletion on populations deprived from
 531 immigration and limited genetic diversity for adaptation
 532 to selective threats, such as warming. Regardless of the
 533 mechanism, it is clear that all threats do cause negative
 534 population growth, and therefore, are capable of driving
 535 populations to extinction.

536 In regards to the effects of warming, it is important to
 537 note that our results indicate that faster warming per
 538 generation, after removing the effect of immigration, led to
 539 faster population declines when compared with slower
 540 warming. These results highlight the importance of
 541 generation time in enhancing adaptation to selective
 542 forces and in explaining why some species have declined
 543 in step with global warming while others have not (e.g.
 544 Parmesan & Yohe 2003). These results also support the
 545 contention that species with long generation times are
 546 more prone to the effects of warming while highlighting the
 547 need to reduce the speed of the current warming trend
 548 (Stenseth *et al.* 2002; Walther *et al.* 2002; Parmesan & Yohe
 549 2003). The overall decline of populations facing any
 550 warming also highlights the sensitivity of ecological systems
 551 to increases in temperature (Poertner *et al.* 2001) and
 552 suggests that environmental heating itself is capable of
 553 causing negative effects on populations independent of
 554 other environmental factors that may change in relation to
 555 warming (e.g. rainfall, currents, productivity, etc.). A
 556 caution in regards to our results is that, given the
 557 environmental gradients in nature, warming can transform
 558 habitats either from suitable to unsuitable or vice versa, and
 559 so may have negative or positive effects on population
 560 density. In our study, population size declined with
 561 warming, suggesting that our results apply to cases where
 562 warming reduces habitat suitability.

563 Quantifying the simultaneous effect of human-related
 564 threats is one of the major challenges in modern ecology
 565 and one of the main worries about the future of
 566 biodiversity (e.g. Myers 1995; Chapin *et al.* 2000; Sala
 567 *et al.* 2000; Novacek & Cleland 2001). Our study provides
 568 an insight into the nature and magnitude of such
 569 interactions. We found that the interaction between
 570 harvesting and reductions in the input of immigration,
 571 which results from isolation of habitats due to their
 572 fragmentation, was additive (i.e. they did not show a
 573 significant interaction). We presume that this may occur
 574 because both of these factors have a similar net effect on
 575 population size through the input and output of individ-
 576 uals. However, the reductions in population size due to

577 these two factors caused synergistic declines in popu-
 578 lations also facing warming. It is probable that the
 579 reductions in population size due to either harvesting or
 580 deprivation of immigration are accompanied with a loss of
 581 genetic diversity, which may impair population resilience
 582 to threats like warming. Importantly, there are empirical
 583 data showing accelerated decays of fragmented (Warren
 584 *et al.* 2001) and harvested (Finney *et al.* 2000; O'Brien
 585 *et al.* 2000) populations facing warming. This suggests
 586 that habitat fragmentation and harvesting do reduce
 587 population resistance to threats such as warming, that
 588 the experimental synergies found here do occur in nature
 589 and that species could be under higher risks of extinction
 590 than those anticipated from single threat analyses. As a
 591 first experimental insight into the effects of harvesting,
 592 habitat fragmentation and warming on population persist-
 593 ence, our study suggests that all threats are equally capable
 594 of causing deleterious effects and that they all have to be
 595 simultaneously reduced, if their synergies are to be
 596 avoided and if the loss of species is to be reversed.
 597

5. UNCITED REFERENCES

598 Holyoak & Lawler (1996) and Molofsky & Ferdy (2005).
 599

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 607

REFERENCES

- 608 Allen, A. P., Brown, J. H. & Gillooly, J. F. 2002 Global
 609 biodiversity, biochemical kinetics, and the energy-equiv-
 610 alence rule. *Science* **297**, 1545–1548. (doi:10.1126/
 611 science.1072380)
 612 Aronson, R. B. *et al.* 2004 Causes of coral reef degradation.
 613 *Science* **302**, 1502–1504. (doi:10.1126/science.302.5650.
 614 1502b)
 615 Botsford, L. W., Castilla, J. C. & Peterson, C. H. 1997 The
 616 management of fisheries and marine ecosystems. *Science*
 617 **277**, 509–515. (doi:10.1126/science.277.5325.509)
 618 Buckley, L. B. & Roughgarden, J. 2004 Effects of changes in
 619 climate and land use. *Nature* **430**. (doi:10.1038/nature
 620 02717)
 621 Carpenter, S. R. 1999 Microcosm experiments have limited
 622 relevance for community and ecosystem ecology. *Ecology*
 623 **80**, 1085–1088. (doi:10.2307/177043)
 624 Chapin, F. S. *et al.* 2000 Consequences of changing bio-
 625 diversity. *Nature* **405**, 234–242. (doi:10.1038/35012241)
 626 Cloberg, J., Dhondt, A. A. & Nichols, J. D. 2001 *Dispersal*.
 627 Oxford, UK: Oxford University Press.
 628 Davies, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B.
 629 & Wood, S. 1998 Making mistakes when predicting shifts
 630 in species range in response to global warming. *Nature*
 631 **391**, 783–786. (doi:10.1038/35842)
 632 Debinski, D. M. & Holt, R. D. 2000 A survey and overview of
 633 habitat fragmentation experiments. *Conserv. Biol.* **14**,
 634 342–355. (doi:10.1046/j.1523-1739.2000.98081.x)
 635 Drenner, R. W. & Mazumber, A. 1999 Microcosm experi-
 636 ments have limited relevance for community and ecosys-
 637 tem ecology: comment. *Ecology* **80**, 1081–1085. (doi:10.
 638 2307/177042)
 639 Fedorov, A. V. & Philander, G. 2000 Is El Niño changing?
 640 *Science* **288**, 1997–2002. (doi:10.1126/science.288.5473.
 641 1997)

- 641 Finney, B. P., Gregory-Eaves, I., Sweetman, J., Douglas,
642 M. S. V. & Smol, J. 2000 Impacts of climatic change and
643 fishing on Pacific salmon abundance over the past 300
644 years. *Science* **290**, 795–799. (doi:10.1126/science.290.
645 5492.795)
- 646 Fryxell, J. M., Smith, I. M. & Lynn, D. H. 2005 Evaluation of
647 alternate harvesting strategies using experimental micro-
648 cosms. *Oikos* **111**, 143–149. (doi:10.1111/j.0030-1299.
649 2005.13840.x)
- 650 Fukami, T. & Morin, P. 2003 Productivity–biodiversity
651 relationships depend on the history of the community
652 assembly. *Nature* **424**, 423–426. (doi:10.1038/nature
653 01785)
- 654 Gause, G. F. 1934 *The struggle for existence*. New York, NY:
655 Dover.
- 656 Grigg, R. W. *et al.* 2005 Reassessing U.S. coral reefs. *Science*
657 **308**, 1740–1742. (doi:10.1126/science.308.5729.1740c)
- 658 Hairston, N. G., Allan, J. D., Colwell, R. K., Futuyma, D. J.,
659 Howell, J., Lubin, M. D., Mathias, J. & Vandermeer, J. H.
660 1968 The relationship between species diversity and
661 stability: an experimental approach with protozoa and
662 bacteria. *Ecology* **49**, 1091–1101. (doi:10.2307/1934492)
- 663 Hanski, I. 1998 Metapopulation dynamics. *Nature* **396**,
664 41–49. (doi:10.1038/23876)
- 665 Holyoak, M. & Lawler, S. P. 1996 Persistence of an
666 extinction-prone predator–prey interaction through meta-
667 population dynamics. *Ecology* **77**, 1867–1879. (doi:10.
668 2307/2265790)
- 669 Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der
670 Linden, P. J. & Xiaosu, D. (eds) 2001 *Climate change:
671 the scientific basis*, p. 144. Cambridge, UK: Cambridge
672 University Press.
- 673 Huston, M. A. 1999 Microcosm experiments have limited
674 relevance for community and ecosystem ecology: synthesis
675 of comments. *Ecology* **80**, 1088–1089. (doi:10.2307/
676 177044)
- 677 Jackson, J. B. C. *et al.* 2001 Historical overfishing and the
678 recent collapse of coastal ecosystems. *Science* **293**,
679 629–638. (doi:10.1126/science.1059199)
- 680 Jenkins, M. 2003 Prospects for biodiversity. *Science* **302**,
681 1175–1177. (doi:10.1126/science.1088666)
- 682 Jessup, C. M., Kassen, R., Forde, S. E., Kerr, B., Buckling,
683 A., Rainey, P. B. & Bohannan, B. J. M. 2004 Big questions,
684 small worlds: microbial model systems in ecology. *Trends
685 Ecol. Evol.* **19**, 189–197. (doi:10.1016/j.tree.2004.01.008)
- 686 Kassen, R., Buckling, A., Bell, G. & Rainey, P. B. 2000
687 Diversity peaks at intermediate productivity in a labora-
688 tory microcosm. *Nature* **406**, 508–512. (doi:10.1038/
689 35020060)
- 690 King, C. E. 1967 Food, age, and dynamics of a laboratory
691 population of rotifers. *Ecology* **48**, 111–128. (doi:10.2307/
692 1933423)
- 693 Kussell, E. & Leibler, S. 2005 Phenotypic diversity,
694 population growth, and informatics in fluctuating environ-
695 ments. *Science* **309**, 2075–2078. (doi:10.1126/science.
696 1114383)
- 697 McGrady-Steed, J., Harris, P. M. & Morin, P. 1998
698 Biodiversity regulates ecosystem predictability. *Nature*
699 **390**, 162–165.
- 700 Molofsky, J. & Ferdy, J. B. 2005 Extinction dynamics in
701 experimental metapopulations. *Proc. Natl Acad. Sci. USA*
702 **102**, 3726–3731. (doi:10.1073/pnas.0404576102)
- 703 Mora, C. & Ospina, F. 2001 Thermal tolerance and potential
704 impact of sea warming on reef fishes from Gorgona island
705 (eastern Pacific Ocean). *Mar. Biol.* **139**, 765–769. (doi:10.
706 1007/s002270100626)
- 707 Mora, C. & Ospina, F. 2002 Experimental effects of cold, La
708 Nina temperatures in the survival of reef fishes from
709 Gorgona Island (eastern Pacific Ocean). *Mar. Biol.* **141**,
710 789–793. (doi:10.1007/s00227-002-0862-1)
- 711 Mora, C. & Sale, P. F. 2002 Are populations of coral reef
712 fishes open or closed? *Trends Ecol. Evol.* **17**, 422–428.
713 (doi:10.1016/S0169-5347(02)02584-3)
- 714 Myers, N. 1995 Environmental unknowns. *Science* **269**,
715 358–360. (doi:10.1126/science.269.5222.358)
- 716 Myers, R. A. & Worn, B. 2002 Rapid worldwide depletion of
717 predatory fish communities. *Nature* **423**, 280–283.
718 (doi:10.1038/nature01610)
- 719 Novacek, M. & Cleland, E. E. 2001 The current biodiversity
720 extinction event: scenarios for mitigation and recovery.
721 *Proc. Natl Acad. Sci. USA* **98**, 5466–5470. (doi:10.1073/
722 pnas.091093698)
- 723 O'Brien, C. M., Fox, C. J., Planque, B. & Casey, J. 2000
724 Climate variability and North Sea cod. *Nature* **404**, 142.
725 (doi:10.1038/35004654)
- 726 Parmesan, C. & Yohe, G. 2003 A globally coherent finger-
727 print of climate change impacts across natural systems.
728 *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- 729 Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J.,
730 Sumaila, U. R., Walters, C. J., Watson, R. & Zeller, D.
731 2002 Towards sustainability in world's fisheries. *Nature*
732 **418**, 689–695. (doi:10.1038/nature01017)
- 733 Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers,
734 P. & Watson, R. 2003 The future for fisheries. *Science* **302**,
735 1359–1361. (doi:10.1126/science.1088667)
- 736 Petchev, O. L., McPhearson, P. T., Casey, T. M. & Morin,
737 P. J. 1999 Environmental warming alters food-web
738 structure and ecosystem function. *Nature* **402**, 69–72.
739 (doi:10.1038/47023)
- 740 Pimm, S. L. & Rave, P. 2000 Extinctions by numbers. *Nature*
741 **403**, 843–845. (doi:10.1038/35002708)
- 742 Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M.
743 1996 The future of biodiversity. *Science* **269**, 347–350.
744 (doi:10.1126/science.269.5222.347)
- 745 Poertner, H. O. *et al.* 2001 Climate induced temperature
746 effects on growth performance, fecundity and recruitment
747 in marine fish: developing a hypothesis for cause and effect
748 relationships in Atlantic cod *Gadus morhua* and common
749 eelpout *Zoarces viviparus*. *Cont. Shelf Res.* **21**, 1975–1997.
750 (doi:10.1016/S0278-4343(01)00038-3)
- 751 Sala, O. E. *et al.* 2000 Global biodiversity scenarios for the
752 year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.
753 287.5459.1770)
- 754 Schiermeier, Q. 2003 Climate findings let fishermen off the
755 hook. *Nature* **428**, 4. (doi:10.1038/428004a)
- 756 Smith, V. H., Foster, B. L., Grover, J. P., Holt, R. D., Leibold,
757 M. A. & DeNoyelles Jr, F. 2005 Phytoplankton species
758 richness scales consistently from laboratory microcosms to
759 the world's oceans. *Proc. Natl Acad. Sci. USA* **102**,
760 4393–4396. (doi:10.1073/pnas.0500094102)
- 761 Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W.,
762 Chan, K.-S. & Lima, M. 2002 Ecological effects of
763 climate fluctuations. *Science* **297**, 1292–1296. (doi:10.
764 1126/science.1071281)
- 765 Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C.,
766 Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O.
767 & Bairlein, F. 2002 Ecological response to recent climate
768 change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- 769 Warren, M. S. *et al.* 2001 Rapid responses of British
770 butterflies to opposing forces of climate and habitat
771 change. *Nature* **414**, 65–69. (doi:10.1038/35102054)
- 772 Worm, B. & Myers, R. A. 2004 Managing fisheries in a
773 changing climate. *Nature* **429**, 15. (doi:10.1038/429015a)
- 774 Yoshida, T., Jone, L. E., Ellner, S. P., Fussmann, G. F. &
775 Hairston, N. G. 2003 Rapid evolution drives ecological
776 dynamics in a predator–prey interaction. *Nature* **424**,
777 303–306. (doi:10.1038/nature01767)

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