Microcosm experiments can inform global ecological problems

Tim G. Benton¹, Martin Solan², Justin M.J. Travis³ and Steven M. Sait¹

¹ Institute of Integrative and Comparative Biology, University of Leeds, Leeds, UK, LS2 9JT
² Oceanlab, University of Aberdeen, Main Street, Newburgh, Aberdeenshire, UK, AB41 6AA
³ Zoology Building, Tillydrone Avenue, University of Aberdeen, Aberdeen, UK, AB24 2TZ

Global-scale environmental problems are rarely regarded as amenable to traditional scientific experiment. We argue here that small-scale experiments using ‘model organisms’ in microcosms or mesocosms can be a useful approach for apparently intractable global problems, such as ecosystem responses to climate change or managing biodiversity through the design of nature reserves. An experimental, small-scale research programme can easily be coupled with the development of theory and act as a stimulus to further research, thereby hastening both understanding of the issues and development of practical solutions. This process – from microcosm experiment to the development of practical application – has previously been influential but also has a long time lag. We suggest short-cuts in an attempt to stimulate the use of small-scale experiments to address globally urgent issues with meaningful policy implications.

Introduction

Anthropogenic environmental change – whether through climate change, habitat fragmentation or degradation – is occurring at an unprecedented rate. This environmental change is affecting biodiversity and the ecological services that species provide to humanity, such as nutrient cycling, pollination, predator control, carbon sequestration and soil fertility [1]. Policies to prevent or mitigate the ecological impacts of environmental change require robust scientific evidence, but the temporal and spatial scales of global environmental problems are sufficiently extensive that mechanistic understanding of cause–effect relationships is difficult to gain, especially through the traditional route of experimental manipulation [2]. However, it is possible to conduct replicated experiments on model systems, with the ease of experimentation increasing as the scale of the model system gets smaller. Experimental microcosms (such as protist systems) or mesocosms (such as many invertebrate and plant systems) might be easy to experiment upon, but there can be a ‘credibility gap’ from within the scientific community, such that insights from these systems are often seen to be irrelevant to understanding larger scale processes. Our thesis in this paper is that this view is mistaken. Small-scale experimental systems – hereafter we will use the term microcosms, but this should be taken to include mesocosms and also small-scale plot or field experiments – have historically informed understanding of ecological processes that are applicable at larger scales. Given the successful track record of this approach, we argue that the use of microcosms can be increased, potentially influencing the understanding of how to deal with apparently intractable large-scale environmental problems. We contend that investigations using microcosms have stimulated theory-development, which has, in turn, stimulated replication in other systems at increasingly extensive spatial and temporal scales, thereby establishing generality and narrowing the ‘credibility gap’. The role of microcosms might, therefore, be crucial in defining a research programme that leads to understanding of large-scale processes, but the time taken to replicate across systems and across different experimental scales is considerable and, in a rapidly changing world, we often need answers in short order and certainly within a time scale that will influence policy. The suggestion we make is to encourage a culture change in ecology and its funding, such that theory development and replication in multiple experimental systems is conducted in parallel instead of sequentially. This requires funding bodies to recognize the value of replication in different systems to gain generality of understanding, rather than the more traditional view of valuing originality as having greater fundamental importance.

Have microcosm approaches been influential?

Model systems (e.g. laboratory microcosms or small-scale field experiments) enable the rigorous testing of ecological theory with replicated experiments on populations or communities [3–5]. Familiar models include protist or protist-rotifer microcosms, invertebrates such as soil mites, beetles, moths and their natural enemies, and plant–herbivore or plant–herbivore–natural enemy systems [6]. In terms of understanding the fundamental principles of ecology, the use of microcosms has a rich and distinguished history [6], including the consequences of demographic and environmental noise [7,8], life history plasticity [9], predator–prey population dynamics [10–12], food-web structure and multi-trophic interactions [13–15], competition and predation [16–19], invisibility and community complexity [20–22], species coexistence [23], and community stability and persistence [24,25]. This, by no means exhaustive, list of accomplishments illustrates how using even simple model systems that comprise few, ‘non-representative’ taxa has nevertheless influenced our understanding of processes that ultimately impact upon
complex ecosystems, and therefore counters the ‘credibility gap’ arising from the fact that protists or insects are not representative of fish or mammals.

Despite their distinct contribution to our understanding of ecology and the environment, however, microcosm approaches are often criticized for being irrelevant for policy-relevant issues [26–27], but see Ref. [28] for opposite viewpoint. This view might stem from the fact that advocates of model systems have, for the most part, been driven by the urge to explore and understand the processes and mechanisms that underpin the fundamental processes of ecology rather than using model systems principally and specifically to address real world, global-scale problems. Furthermore, the ease with which mechanisms can be dissected under controlled conditions has sometimes led to an understanding of intrinsic processes that might be of scientific interest, but actually is of debatable relevance to ecology in the ‘real world’. This can be caricatured by saying that microcosms have often provided the right answer to the wrong question. For example, Park’s classic demonstration of competitive exclusion in flour beetles in carefully controlled, constant and equilibrium conditions [29] led to an expectation that the same processes would be common in the natural world and, therefore, that ‘co-existence’ of similar species was an enigma. Developing our modern concept of dynamic and complex webs, in which co-existence is a simple by-product of temporal and spatial variation, might arguably have been held back by the ‘equilibrium’ world view engendered by microcosm experiments coupled with simple deterministic models. Similarly, the observation of dynamical chaos in simple mathematical models led to the valid question about whether chaos underpinned the complex population dynamics often observed in time series data. Chaos in population dynamics was first of all demonstrated within the beguiling simplicity of a laboratory microcosm [30] and for a while such results supported a view that as chaotic dynamics were empirically observed they might also be common, or even necessary, to explain complex dynamics in the field. This view is mistaken (and perhaps led to some wasted research effort) because the interaction between environmental and demographic stochasticity and determinism, revealed by more recent theory and laboratory experiments [7,8,31,32], is perhaps the most parsimonious explanation for noisy dynamical patterns. That model systems can be used to understand deterministic processes that might be ‘too simple’ to apply to the real world does not invalidate their utility in asking questions that are directly relevant to field-based ecological questions. Devotees of the model system approach need only change the focus of their questions from a concentration on ‘blue-skies’ and fundamental issues to one addressing more realistic ecological scenarios or policy-relevant questions. For example, ecology in the real world is not deterministic, but is strongly influenced by stochastic processes. This realization has led to microcosms being increasingly used to explore ecology in more realistic stochastic environments [8,33]. Indeed, more recently, the use of microcosms has had a role in exploring the consequences of seemingly insurmountable global issues, such as the effect of climate change on species distributions and food-web structure [34,35], the effects of biodiversity loss on ecosystem functioning [36,37], and the impacts of pollution and fisheries on ecosystems [38] or harvesting on population dynamics [39].

An important reason why microcosms are so influential is that they provide a mechanistic, rather than a phenomenological, understanding of ecological processes and therefore have a disproportionate influence on the development of theory. Models, either mathematical or computational, are always based on sets of assumptions, and these assumptions must be developed with reference to biological understanding. Microcosms can supply some of the necessary biological understanding and deep understanding (and therefore more certain predictive power) comes from theory that incorporates the proper biological or ecological mechanisms. Such mechanisms can always be assumed, but information to support or test the assumptions can most easily be developed from simple experiments designed to gain the required mechanistic knowledge. Of course, we recognize that traditional factorial experiments are not the only way to develop an understanding of mechanism. For example, meta-analyses and Bayesian statistical approaches to model fitting can inform ecological theory using data from multiple systems [40]. Such approaches are not dissimilar to that which we propose in that both encourage the simultaneous and parallel accumulation and gathering of evidence from multiple sources. Furthermore, advocates of such statistical inference techniques would concede that empirical testing is still one important component of the approach because construction of models still relies on careful experimentally derived parameter estimates of ecological processes. We suggest that microcosms have two important roles in the future development and utilization of these modern quantitative approaches. First, they provide ideal systems on which the statistical approaches can be tested, enabling proper assessment of the likely information demands of the models: a key question will be how much does understanding of the processes involved determine the amount of data required in order for sound predictions to be made? For example, using microcosm-derived data one can successively add more biological information into a model to assess how much ‘mechanism’ is required to capture successfully the system’s behavior. Second, increasingly, we will be asked to provide management recommendations on systems for which we have limited existing knowledge of the ecological processes involved. Information on processes derived from microcosm studies could be used as ‘prior’ knowledge in a Bayesian approach in lieu of, or wherever possible together with, field-based evidence, and is likely to increase our predictive capability.

Although the use of model systems might appear to be limited in scope and realism, especially compared with the infinite complexities of the real world and the spatial extent of global scale problems, the utility of the microcosm approach lies in its ability to explore and test mechanisms. Although such systems are far removed from real-world complexities, they provide the first hurdle for models – if theory cannot explain microcosm data, it will have no credibility in the field. Curiously, despite the potential danger of extrapolating from untested, or untestable,
mathematical model predictions *alone* to real world issues, this approach has often been readily accepted by policy makers [41]. We suggest that the potential danger of extrapolating simple laboratory systems to the real world only becomes apparent if such systems are the *raison d’etre* and sole focus for the research, becoming isolated from natural world phenomena in the process. It is clear that microcosm studies, modelling and field experimentation need to develop synchronously.

**Can microcosms inform policy-relevant issues?**

The influence of microcosms on understanding ecological processes in the field (or on understanding those pertinent to management issues) is often under-appreciated because there is a considerable lag between microcosm studies and their eventual impact on applied or large-scale ecology (Box 1). This lag reflects a gradual process whereby microcosm experiments stimulate the development of theory, which then stimulates the testing of theory on different systems, typically followed by a refinement of theory, then by a further test of theory at larger spatial scales (e.g., in field-plots), and so on. The common view is that only after this protracted process is sufficient generality mustered to demonstrate understanding at a level deemed suitably robust to be applied to management and policy. Waiting until the credibility gap is closed is the safest option but, in a rapidly changing world, doing so forms a risk averse strategy that assumes that time is on our side and ignores portfolio theory [42]. Here, policy makers can reduce risks to human well-being purely on statistical grounds by making recommendations based on several sources of information, albeit if some of these are unreliable or incomplete, rather than advocating policy change based only on firm evidence that meets a certain

---

**Box 1. The influence of microcosms on applied science exists but is lagged**

Work on microcosms (interpreted broadly as experimental ecological systems at a small spatial scale) is influential because it provides a route to mechanistic understanding, such as is required to test or develop theory. Microcosms therefore might be influential in applied ecology by stimulating the theoretical underpinnings of the science, and prompting a cascade of theory, tests in different model systems and at different spatial scales before becoming general enough to influence applied science. To investigate the time scale of this ‘cascade’ we analysed the citation lag to a cutting-edge theoretical journal (*The American Naturalist*) made in three journals (representing a gradient from theoretical ecology to applied conservation) between 2003 and 2006. In this example, the time lag from theoretical ecology to its adoption in practice, in terms of peak citation number, is 15–17 years (Figure I). This analysis also implies that applied science is relying on theory that is perhaps outdated.

Investigating this in greater detail, we analysed the pattern of citations for a single influential paper that was key to the development of the biodiversity-ecosystem function field of research, and which has fundamental policy relevance with respect to biodiversity loss (Naeem et al. 1994) [49]. Immediately following publication of the paper, discussion led to the development of theory and methodology, then laboratory mesocosm and field manipulations and observations have become increasingly common as time has elapsed (Figure II).

---

**Figure I.** The percolation of theory through the scientific literature can be observed by comparing the citation lag between papers published in a theoretically orientated journal (*American Naturalist*), a conservation science journal (*Conservation Biology*) and a management-orientated journal (*Journal of Wildlife Management*). Note the progression in time in the peak citation delay between each journal, indicating the lag of time that occurs between developing the latest theory (*American Naturalist*), applying it to conservation issues (*Conservation Biology*) and implementing it in real world applications (*Journal of Wildlife Management*). All papers listed in the ISI Web of Science in the three journals were assessed from 2003–2006 and all citations to *American Naturalist* were tallied for the different time points. Sample sizes: *American Naturalist* citations of *American Naturalist* = 3038 (red bars), *Conservation Biology* citations of *American Naturalist* = 316 (orange bars), *Journal of Wildlife Management* citations of *American Naturalist* = 99 (yellow bars).

---

**Figure II.** The percolation of ideas from a single study over a decade. Citations to Naeem et al. (1994) [49], from publication to December 2006 (n = 524), were assigned to categories that reflect how the information contained within the paper was used in subsequent publications. The paper [49] is one of the most highly cited contributions to the biodiversity-ecosystem function research field and the conclusions of this paper were either discussed (red), used to develop or reinforce new theory (orange) or methodology (yellow), initiate or inform laboratory microcosms (green), field manipulations (turquoise) or observations (blue), or used as a basis for the practical application of theory in the real world (pink). The perceived level of credibility increases with time as citing authors build on previous capacity, such that there is an evolution from discursive contributions in the literature to application in the real world via the intermediate categories. This process takes more than a decade and forms the mechanistic sequence that underpins the percolation of ideology through the literature.
credibility criteria. The question is not one of whether microcosms can inform policy, but why the conclusions from simple laboratory systems are so readily dismissed from the portfolio of evidence?

The problem of credibility can be illustrated with a contemporary example where microcosms are being extensively used to explore the consequences of biodiversity loss on ecosystem processes [43,44]. This has been a key issue in recent years because of the profound implications the loss of biodiversity might have for human well-being, particularly in regions containing the least privileged sectors of society [1]. Microcosm experiments that have manipulated species richness in terrestrial and aquatic environments indicate that biodiversity in its broad sense matters for the provision of ecosystem processes [1,36,37,43,44], a conclusion that is consistent with general scientific opinion [45], correlational evidence and anecdotal observations [46]. Nonetheless, there is wide variation in how ecosystems respond to species extinction, raising problems with deriving general conclusions [2,27]; however, the growing body of evidence is increasingly enabling more powerful analyses [36,37]. It is important to realize, however, that such criticism does not undermine the validity of the hypotheses that are being tested in microcosms, rather it points to cultural differences in approaches between disciplines [47], the inherent difficulty in identifying and attributing causal mechanisms associated with changes in biodiversity, and the need to acknowledge the limitations of each study [27,48]. Focusing on these issues and what the research community is yet to establish forms a distraction from the main research agenda, and is likely to have a negative effect on presenting a case for support based on what we do know to policy makers. For example, we do know from microcosm experiments that functional traits matter most [49], and that the way ecosystems respond to species extinction depends on both the cause of extinction and, crucially, the order in which species disappear [50]. Knowledge of this kind is vital to the formulation of policy and management strategies, and has immediate implications for the conservation of biological resources and habitat before further dramatic changes in atmospheric carbon dioxide, climate, vegetation and land use occur as a result of anthropogenic activity [51]. Excluding such evidence in lieu of achieving full credibility status is hard to reconcile given the time sensitive nature of global problems.

A generic solution to utilizing microcosms for large-scale ecological questions

The ability to identify intrinsic mechanisms makes the microcosm approach a powerful tool, but the ‘credibility gap’ of small spatial scale and controlled conditions, and that microcosms typically use different taxa than those of primary interest, needs to be overcome more quickly than waiting for the diffusion of results across systems, from laboratory to field to application (Box 1).

Here, we suggest that this credibility process would be short-cut by the immediate coupling of theory, observation and experiment, and near-simultaneous replication across systems to establish generality. An effective response to current global issues demands an approach to research that has a consortium enterprise and a change of culture, both in terms of funding (intersystem, interdisciplinary and international) and research ethos (to replicate rather than seek novel answers). We provide two timely examples to illustrate this principle. Both are especially relevant in terms of their important application, with clear policy and social implications, and both need to be underpinned by fundamental science.

Reserve selection and refuges in the context of fisheries

The extent to which no-fish zones or marine protected areas (MPAs) ameliorate the effects of overfishing remains unresolved [52]. Theory predicts that MPAs can lower the risk of stock collapse with a minor reduction in maximum sustainable yield, but experimental field tests of the generality of the theory at the scale of whole fisheries are impossible to achieve with true replication. By contrast, networks of microcosm populations can be established as an analogue of a marine reserve and the effect of harvesting on local yields and the resilience of the overall system assessed, making the theory open to empirical test and refinement. Moreover, evolutionary consequences can be measured and evaluated at realistic timescales [53]. Such microcosms can generate results efficiently and can be replicated across a range of model organisms (both invertebrates and vertebrates, in the laboratory, and at a larger scale in the field in tanks or ponds) with different demographic characteristics and developed further to ask more complex questions, such as the ideal design and location of reserves in a variable environment. The results from the model systems can be used both to develop theory and test the utility of predictive models, and so lead to policy recommendations that can be extrapolated to natural systems at a scale capable of bridging the perceived credibility gap between laboratory experiments and the field [54,55]. It is relatively easy to manipulate protist and invertebrate systems in the laboratory, and possible, but more difficult, to manipulate fish systems in tanks or pools. We suggest, therefore, that theory is developed and tested using the simplest systems that enable many generations to be tracked, and this theory then can be tested using fish in more simple experiments in tanks or pools. That way, the theory makes fewest untested assumptions and if it predicts the response of fish it gains appropriate credibility to the appropriate taxon.

If theory developed using results easily generated from protist and invertebrate systems in the laboratory can predict the responses from fish kept in tanks or ponds, then the theory can have greater credibility than if it were developed using untested assumptions.

The distribution of species in response to changes in climate variables

Most field ecologists and species’ distribution modellers believe that changes in atmospheric carbon dioxide could have a profound impact on species’ distributions, but addressing this empirically in the field is seen as intractable [56] even though notable examples exist [57]. This contrasts markedly with our understanding of the responses of species to changes in temperature [35,58,59]. The lack of even simple predictions for the affects of changing CO₂ leaves

www.sciencedirect.com
us uncertain about whether species distributions and population dynamics have already been affected, or even how to incorporate the potential impact of CO₂ levels, and their interaction with other climate variables, into distribution models for individual species.

Microcosm experiments could examine the population dynamics and evolutionary responses of several short-lived plant species over several generations in response to three environmental factors: temperature, precipitation and CO₂ (from pre-industrial to predicted future worst-case scenarios). Such an experimental programme, which could be completed in 3–5 years, would identify how CO₂ levels affect the position of species along temperature and moisture gradients. This information would identify parts of the world where species might be predicted to move into drier or wetter areas, and, if the predictions are met, would facilitate the adjustment of model projections of species distributions given different CO₂ futures.

Conclusions

If we are to derive fully the benefits of coupling powerful experimentation with theory and real-world observations in time to mitigate immediate large-scale global problems, closing the credibility gap demands a fundamental change in scientific funding and scientific culture. Despite perceived wisdom, we argue that apparently intractable global research problems associated with the environment are amenable to quick, efficient, small-scale experiments. The inherent time lag associated with the credibility process can be short-cut by the parallel development of theory, observation, experiments and replication across systems to establish generality. Such an approach will stimulate larger-scale field research, and hasten both understanding of the issues and development of practical solutions. The culture change required would be that investigators (and funding bodies) see the benefit of simultaneous replication of experiments across different systems, in order for the generality of results and theory to be established and thereby short-cut the traditional process of sequential investigations over many years. This requires the community to value replication of investigations more highly than we currently do, where our science is often driven more strongly by ‘novelty’.

Acknowledgements

This report was derived from a workshop on ‘The application of microcosm approaches and modelling to species responses to environmental change’, funded by the Natural Environment Research Council and English Nature (Agreement R6-H12–01) within the UK Population Biology Network (awarded to T.G.B. and S.M.S.). We are grateful to Colin Beale, Mike Bonsall, Stephen Cornell, Calvin Dytham, Rob Freckleton, Mikko Heino, Greg McNerney, Bill Kunin, Stuart Piertney and Chris Thomas for their stimulating and insightful discussions held during the workshop, which forms the intellectual basis for this article.

References

37 Balvanera, P. et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9, 1146–1156

Have you contributed to an Elsevier publication? Did you know that you are entitled to a 30% discount on books?

A 30% discount is available to all Elsevier book and journal contributors when ordering books or stand-alone CD-ROMs directly from us.

To take advantage of your discount:

1. Choose your book(s) from www.elsevier.com or www.books.elsevier.com

2. Place your order

   Americas:
   Phone: +1 800 782 4927 for US customers
   Phone: +1 800 460 3110 for Canada, South and Central America customers
   Fax: +1 314 453 4898
   author.contributor@elsevier.com

   All other countries:
   Phone: +44 (0)1865 474 010
   Fax: +44 (0)1865 474 011
directorders@elsevier.com

   You’ll need to provide the name of the Elsevier book or journal to which you have contributed. Shipping is free on prepaid orders within the US.
   If you are faxing your order, please enclose a copy of this page.

3. Make your payment

   This discount is only available on prepaid orders. Please note that this offer does not apply to multi-volume reference works or Elsevier Health Sciences products.

   For more information, visit www.books.elsevier.com