

tinental crust as any we know. That does not imply that chemical and physical differentiation into core, mantle and some sort of predominantly mafic proto-oceanic crust did not occur well before  $\sim 4,000$  Myr ago. Such a world-wide proto-crust, studded with countless small rifts and volcanic islands emitting voluminous ultramafic, mafic and relatively minor acid lavas, provides a very different scenario from one involving early formation of thick calc-alkaline continental crust. Moreover, chemical and petrological considerations render it most unlikely that crystallization of some very early global magma ocean could directly produce the continental crust<sup>12</sup>.

The ANU workers<sup>1</sup> make no extravagant claims in this matter, and simply state that pre-3,800-Myr silica-saturated rocks must have occurred on the Earth's crust, because zircon is almost always found in such rocks. I fear that some workers may prematurely interpret this to mean 'continental' rocks. We know from Isua, however, that 3,800-Myr-old silica-saturated volcanic rocks (metaryholites) carry rather abundant accessory zircon, whilst I have myself observed zircon in  $\sim 10$ -Myr-old granophyre intrusions in Iceland, which is not a continental environment by any stretch of the imagination. One swallow does not necessarily make a summer, and four zircon grains from a single quartzite sample do not necessarily make a continent.

Finally, there is still a possibility that the 4,100–4,200 Myr ages might be an artefact generated by the combined effects of uranium loss from an  $\sim 3,700$ -Myr-old zircon during a later metamorphic episode at around 3,300 Myr and loss of radiogenic lead comparatively recently. The authors briefly argue against this possibility, but I feel that many workers will require further convincing about this. In the meantime, I understand that the search is on for intact remnants of the 4,100–4,200-Myr-old source rocks of the super-ancient zircon grains in the Mount Narryer quartzite: that embarrassing little gap of 700 Myr between 4,500 and 3,800 Myr badly needs to be substantially narrowed down, preferably by finding some rocks *in situ*. □

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## Ecology

# Laboratory, field and natural experiments

from Jared M. Diamond

THREE experimental approaches to understanding species abundances and distributions have for some time coexisted uneasily in ecology: laboratory experiments, field experiments and natural experiments. Recent papers by Schoener and colleagues<sup>1–4</sup> constitute important advances in applying two of these methodologies, as well as in clarifying the relative strengths and weaknesses of all three.

The virtue of laboratory experiments is of course that values of independent variables are at least in theory completely controlled. The main uses of the approach have been for detailed studies of two-species interactions and of a single species' behavioural responses. (The technique is often practised on microorganisms kept in bottles, hence the ecologists' term 'bottle experiment'.) Well known bottle experiments include those of Gause<sup>5</sup>, Crombie<sup>6</sup> and Park<sup>7</sup>, who studied coexistence conditions and competition between pairs of protozoan or invertebrate species utilizing similar foods. Sheppard<sup>8</sup> and Heller<sup>9</sup> used laboratory cages to study aggressive interactions between two chipmunk species which field observations had suggested to be competitors. Donald<sup>10</sup> grew two plant species in pots with aerial or soil partitions in order to separate the contributions of root and shoot interactions to competitive depression of growth.

A major weakness of this approach in ecology is that most ecosystems depend on so many species and physical variables that laboratory models become uselessly unrealistic. For example, the bottle experiments of Gause and successors told nothing about whether competition is important in natural populations. It is not even possible to know what variables are worth putting into one's bottles until their importance in nature has been established by other means. Furthermore, for most species it is difficult or impossible to keep populations alive and reproducing for many generations under laboratory conditions ('Competition between condors and vultures: a 10-generation cage experiment').

Field experiments are more realistic but at the cost of experimental control. In a typical field experiment a single variable is manipulated — a particular species is removed or fenced out, or a new one is locally introduced (for example, to a small island). The experimenter controls nothing else after selecting manipulated and unmanipulated sites.

One of the first field experiments was by Darwin<sup>11</sup>, who demonstrated that mowing

or introduction of grazing animals increased plant species diversity on a lawn (by preventing some species from outcompeting others). The most extensive introduction experiment is by Schoener and Schoener<sup>3</sup>, who placed lizards on 30 Bahamian islets without lizards and thereby demonstrated that lizards could reproduce successfully on islets much smaller than those supporting lizards naturally.

The weaknesses of field experiments are at least fivefold. First, the outcome of the experiment may vary with year, season and location, because the outcome depends on uncontrollable variables such as weather and uncontrolled predators or competitors. For example, removal of desert lizards<sup>12,13</sup> and rodents<sup>14</sup> either succeeded or failed completely to affect abundances of competing species, depending apparently on rainfall and hence food availability in the particular year of the experiment.

Second, most field experiments are not run for enough generations of the species studied to test for the possibility of such variation (see discussion in ref. 1). Often, the outcome cannot be cured by diligently running the experiment a few more years before publishing. For example, the reason why natural lizard populations are lacking on small Bahamian islands where experimental introductions of lizards routinely succeed is that hurricanes wipe out the occasional self-introduced population every century or so<sup>3</sup>. Biological systems depend on species' genetic properties, yet genetic changes following experimental manipulations may require centuries or millenia.

Third, the spatial as well as temporal scale of many important ecological phenomena bars them to experimental study. For example, distributional evidence shows that habitat fragmentation leads to selective extinction of certain species<sup>15–19</sup>. This process can be demonstrated experimentally in very small areas within short times (for example, by counting insects on pruned mangrove trees for several years<sup>20</sup>). However, some other approach is required to understand why many bird and mammal populations failed to survive 10,000 years on large land-bridge islands fragmented off the continents by rising post-Pleistocene sea level, and to predict which bird and mammal populations will survive a long time in forest fragments made national parks<sup>16,17</sup>.

Fourth, in any ecosystem consisting of three or more species the effect of sustained manipulation of species A on species B depends not only on the direct interaction between A and B but also on their interac-

tions with any other species. Thus, the experimental outcome does not permit unequivocal conclusions about the A-B interaction itself<sup>21</sup>. For example, if B competes with C and if A eats both B and C but prefers B, removal of predator A may paradoxically exterminate its prey C! This fact explains the result of Darwin's classic experiment showing lower plant species diversity on lawns not grazed by sheep. The same interpretation is relevant to the otherwise puzzling outcome of a more recent experiment, in which removal of zooplankton grazers dramatically increased the abundance of certain grazed algae while decreasing others<sup>22</sup>.

Finally, for many species in many places, the merits and drawbacks of field experiments become academic: local removal or introduction of species would be technically impossible, morally reprehensible and politically forbidden.

Natural experiments escape most of the drawbacks of field experiments, at the cost of sacrificing all manipulative control of variables. Instead, control is exercised solely through site selection. The experimenter's aim is to select sites that differ naturally in the presence or absence of one major factor relevant to the dependent variable but which are similar in other major factors.

Typical examples are studies comparing the abundance, morphology, and habitat range of species A on multiple islands, some of which have and others of which lack its competitor or predator species B. For example, Schoener and Toft<sup>2</sup> found that spiders were about 10 times more abundant on average on 48 Bahamian islands without lizards than on 26 with lizards, because lizards prey on and also compete with spiders. Brown<sup>23</sup> found that two species of chipmunk (*Eutamias*, Sciuridae) divide the forest transect altitudinally on numerous Nevadan mountains where they occur sympatrically, but that each species occupies the entire transect on a mountain where it occurs without its competitor.

Natural experiments have three types of advantage. First, they permit one to gather data far more quickly than is possible by field experiments. Thus, one can census more individuals, species, places and times, thereby increasing the scope and reliability of one's conclusions. For example, Schoener and Toft<sup>2</sup> surveyed five spider species on 93 islands with and without lizards in 20 days of field work. In the same time they would have been able to remove most (not all) individual lizards on only two islands lacking them, and they would still have had to wait up to several years for spider densities to reach new equilibrium values on the manipulated islands.

Second, natural experiments permit one to examine conditions that cannot, may not, or should not be created experimentally. For example, Brown could not have succeeded in exterminating chipmunks on a whole mountain. Furthermore, his cons-

quence and the US Fish and Wildlife Service would have prevented him from trying.

Finally, natural experiments reveal the end results of ecological and evolutionary processes operating over long times and large areas. On the one hand, underlying processes such as predation and competition are likely to vary in intensity among seasons or years, and it might happen that a field experiment was done at the wrong time to detect the process<sup>12-14</sup>. On the other hand, a species excluded from a habitat for many generations by a competitor or predator may lose its genetic adaptations for that habitat. Thus, removal of the competitor or predator in a short-term field experiment would not permit reoccupation of the habitat. Only the natural experiment comparing habitats occupied on islands with or lacking the competitor (or predator) for millennia reveals the niche shift<sup>24</sup>.

The obvious weakness of natural experiments is that the observer does not create a known difference between two situations, but must instead decide what difference between two existing situations is the salient one. There is always the risk that some difference other than that recognized by the observer might be the salient one: some unnoticed predator, parasite, soil nutrient, or unspecified factor confined to one of the two situations<sup>25,26</sup>. In science, one can never rule out the possibility that a phenomenon is due to some unspecified factor rather than to an observed correlation: the best one can do is to strengthen the observed correlation and weaken likely alternatives. For example, Schoener and Toft<sup>2</sup> used multiple analysis of covariance of spider densities on 74 islands to disentangle the effect of lizard presence from concurrent effects of island area, isolation and vegetation complexity. Yeaton and Cody<sup>27</sup> showed that song sparrow territory size on islands increased with number of competing species in a way not explained by varying food density and habitat structure, but predictable by considering the identities of the competitors and their similarity to song sparrows in ecology, morphology and behaviour. Schoener's quantitative analysis of habitat shifts in four lizard species was based on 20 sites supporting nearly all existing combinations of these species and sorted out effects of site differences in vegetation<sup>28</sup>. Schoener was thereby able to determine not only by how much each species affected each other species, but also how the effect varied among age and size classes of a species. In such cases it strains one's credulity to argue that the explanation might nevertheless be some unspecified factor.

Recent studies using these three different types of ecological experiment have been useful in dispelling some earlier misunderstandings.

First, there has been concern that the choice of experimental method might be critical to the conclusions reached — especially, that conclusions about the role

of competition might be an artefact of natural experiments and might not be sustained by field experiments. In fact, of about 164 field experiments carried out by the end of 1982 to test for competition, 148 confirmed it<sup>1,29</sup>. It now appears that varying conclusions about the relative roles of competition and predation in nature are not an artefact of varying experimental method. Instead, they reflect an important biological generalization about how the size and trophic status of a species, and the intensity of physical disturbance in its habitat, control its relative sensitivities to competition and predation<sup>1,25,30</sup>.

Second, some proponents of each method have claimed that their method is inherently superior and is the method of choice. In fact, each method has virtues, weaknesses and limitations of scope that vary with the species studied and with the questions asked. This situation in ecology reminds one of the coexistence within atomic physics of research based on astronomical observation and Earth-bound experiments. In ecology as in other fields, availability of very different methodologies can be a source of strength rather than of disunity: conclusions tested by different methods are more robust. □

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#### ERRATUM

In the *News and Views* article by A.L. Bloom on 'Benefits of cloning genes for clotting factors' (*Nature* **303**, 474), the penultimate paragraph should have read 'Biogenetic expression of haemostatically effective factor VIII is another matter. . .'. It is unlikely that bacteria would be able either to carboxylate glutamate residues or to carry out the post-transcriptional glycosylation required to produce functional factor VIII, although production in yeast remains a possibility. We apologise for the error and thank Dr A.D. MacNicoll for pointing it out.