tions with any other species. Thus, the experimental outcome does not permit unequivocal conclusions about the A–B interaction itself[21]. 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[22].

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[2] 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[23] 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[2] 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 conscience 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[12-14]. 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 millenia reveals the niche shift[24].

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[25,26]. 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[2] 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[27] 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[28]. 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[1,29]. 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[1,25,30].

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. □

Jared M. Diamond is Professor of Physiology at the University of California Medical School, Los Angeles, California 90024.

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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 possiblity. We apologise for the error and thank Dr A.D. MacNicoll for pointing it out.