consists of about 10 species) and taxa that were determined as close relatives in a complete analysis of Rhamnaceae[18]. The data matrix containing the aligned sequences is available on request from the J.E.R. All sequences have been submitted to GenBank (accession numbers AJ327603–327621, AJ328801–328835, AJ225798, AJ225803, AJ390350, AJ390352–390353, AJ390356–390358, AJ390361, AJ390363). The species included here are a subset of those in a larger matrix and represent each of the lineages identified (F.M.W., J.E.R., M.F.F., Q.C.B.C., M.W.C. and H.P.L., unpublished work).

Phylogenetic analysis

Data were analysed using the parsimony algorithm of the software package PAUP* version 4.0d64 for Macintosh[19]. Tree searches were conducted under the equal and unordered weights criterion (Fitch parsimony)[20] with 1,000 random sequence additions and tree bisection reconnection branch swapping. One thousand replicates of the bootstrap[21] were used to estimate tree stability. Parsimony analysis of both separate and combined data sets produced trees with the same topology and high bootstrap percentages for all lineages that affected the dating. The combined analysis produced only six shortest trees, among which differences involved variation in portions of the trees not important to the conclusion reached here (for example, within the core clades of *Phylica*).

Molecular clock calibration

Rate heterogeneity among lineages was evaluated for the ITS data set using the likelihood ratio test[22], which compares log likelihoods of both constrained and unconstrained hypotheses. We used a three-parameter, maximum-likelihood model with transition/transversion ratio and gamma distribution of rate variation among sites estimated from the ITS sequence region. The molecular clock was rejected because the constrained and unconstrained analyses were significantly different (4,905.3 versus 4,827.3; $P < 0.005$), so Sanderson's method of nonparametric rate smoothing (NPRS)[23] was applied to produce an ultrametric tree using TreeEdit version 1.0 alpha 4-61 (ref. 24). We used the ITS data optimized on the combined tree (shown in Fig. 1) to calibrate the tree at two nodes in absolute time: (1) a date of 2 Myr ago was used to define the split (node I, Fig. 1) between the Mauritian and Réunion populations of *Phylica nitida* (both shown with DNA fingerprinting by AFLP analysis to be monophyletic; J.E.R., M.F.F., Q.C.B.C. and M.W.C., manuscript in preparation); (2) a date of 14.3 Myr ago was used to define the split (node B; Fig. 1) of the sister clade of *Phylica* and that of *Phylica* itself. We also determined the confidence intervals for these dates by keeping the tree fixed and bootstrapping the data set 100 times, each time estimating the divergence time on this single fixed tree; this allowed us to construct a histogram of the possible divergence times (Fig. 2). The length of the NPRS branch of *P. nitida* on Réunion enabled us to infer dates for the other nodes within the phylogenetic tree for *Phylica* and related taxa. *Noltea* (node A) split from the *Phylica* lineage 15–18 Myr ago. Node B, that of *Nesiota* and *Trichocephalus* relative to *Phylica*, dates to 12–15 Myr ago, which accords well with the putative dispersal of the ancestor of *Nesiota* to St Helena, the origin of which is dated at 14.3 Myr ago. Node C, at 7–8 Myr ago, which is the one marking the onset of species diversification of *Phylica* in the Cape, parallels the point at which rapid aridification in the Cape began. Node H occurred at 1.5–2.5 Myr ago, which accords well with the age of the youngest islands on which *P. arborea* is endemic in the southern oceans. Dates of nodes calibrated from the most parsimonious tree (uncorrected branch lengths) provide older age estimates, but these fall within those calculated from the bootstrap of the NPRS tree. NPRS is known to be inaccurate if sequence divergence is low (which is true for the first calibration point used above, but not for the second one deeper in the tree), so we also estimated dates without NPRS (based solely on the maximum-likelihood estimate of branch lengths). These results all fall within the confidence intervals estimated by the bootstrapping procedure. Our conclusions about the timing of the *Phylica* radiation and its connection to the most recent period of aridification are thus supported regardless of the method of estimation used; we prefer the dates from NPRS because we know that rate heterogeneity is present in these ITS data, and the dates presented above and in Fig. 1 are the NPRS dates.

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Predators increase the risk of catastrophic extinction of prey populations

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There has been considerable research on both top-down effects[1,2] and on disturbances[3–5] in ecological communities; however, the interaction between the two, when the disturbance is catastrophic, has rarely been examined[6]. Predators may increase the probability of prey extinction resulting from a catastrophic disturbance both by reducing prey population size[7,8] and by changing ecological traits of prey individuals such as habitat characteristics[8,9] in a way that increases the vulnerability of prey species to extinction. We show that a major hurricane in the Bahamas led to the extinction of lizard populations on most islands onto which a predator had been experimentally introduced, whereas no populations became extinct on control islands. Before the hurricane, the predator had reduced prey populations to about half of those on control islands. Two months after the hurricane, we found only recently hatched individuals—apparently lizards survived the inundating storm surge only as eggs. On predator-introduction islands, those hatchling populations were a smaller fraction of pre-hurricane populations than on control islands. Egg survival allowed rapid recovery of prey populations to pre-hurricane levels on all control islands but on only a third of predator-introduction islands—the other two-thirds lost their prey populations. Thus climatic disturbance compounded by predation brought prey populations to extinction.

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The experiment, which was punctuated by the hurricane, began in April 1997 when the large predatory lizard *Leiocephalus carinatus* was introduced onto five islands that already had populations of a smaller lizard, *Anolis sagrei*. Six other islands with *A. sagrei* populations served as controls; we also monitored an island that *L. carinatus* had invaded naturally shortly before the experiment began; this island is counted with the islands that were experimentally invaded by *Leiocephalus carinatus* below. *Leiocephalus carinatus* colonist lizards were collected from the mainland of Great Abaco, the Bahamas, using sites ranging from the parts of the mainland that are very close to the study islands to areas up to 12 km away.

The larger species of lizard, which is known to consume the smaller *A. sagrei*[10], had immediate and dramatic effects on the invaded species. Although introduction and control islands averaged similar numbers of *A. sagrei* at the beginning, the population size on islands where *L. carinatus* was introduced dropped markedly, levelling off at about half the control value (Fig. 1a). The smaller species shifted its habitat upwards in the vegetation, eventually occupying the higher and thinner branches (Fig. 1b), which the larger species mostly avoided. Pre-hurricane results of this experiment are being reported elsewhere[11].
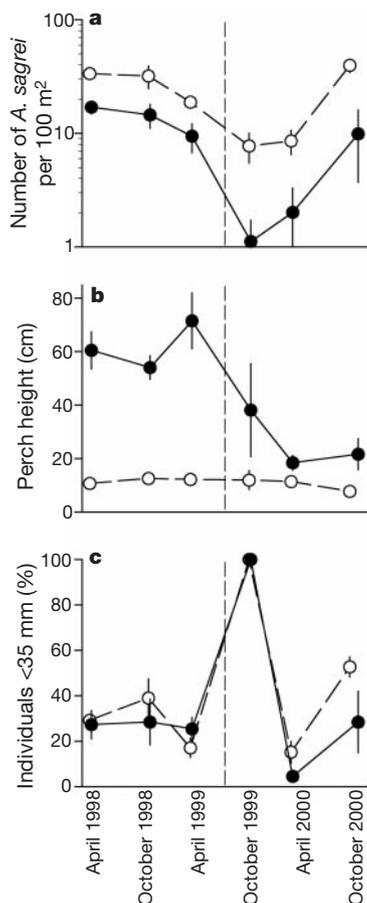

Figure 1 Properties of populations of the lizard *Anolis sagrei* before and after hurricane Floyd. Vertical dotted line marks the occurrence of the hurricane. Open circles, *Leiocephalus carinatus* absent; closed circles, *L. carinatus* introduced. **a**, Density of *A. sagrei* on the two categories of study islands (with and without the larger predatory lizard). **b**, Perch height of *A. sagrei*. **c**, The fraction of very small *A. sagrei* individuals, that is, those likely to have hatched from eggs within the past two months. In another study[11], we showed that *L. carinatus* significantly reduced the smallest (<29 mm) lizards; here, using a size of <35 mm, a similar difference is apparent at most dates except the one immediately after the hurricane, when all individuals in both treatments are small. We note that the first year of the pre-hurricane portion of the experiment is not shown.

On 14 September 1999, Floyd, a category-IV hurricane with maximum sustained winds of around 250 km h^{-1} and an approximately 3-m storm surge passed directly over the study site. Two months later, 13–19 November, we saw 65 different individuals of *A. sagrei* on all 12 study islands combined; none was larger than 34 mm and only one was larger than 32 mm, a dramatic contrast with a typical year's distribution in size of individuals (Fig. 1c). Thus the post-hurricane lizard populations consisted entirely of juveniles! Figure 2 illustrates the huge change that the hurricane wrought upon the size-frequency distribution of *A. sagrei*. (That this post-hurricane cohort was growing up in the total absence of adults is not necessarily deleterious, as *A. sagrei* has no parental care and indeed shows occasional cannibalism[12].) Although only three individuals of the large species, *L. carinatus*, were seen (one on each of three islands), these were also relatively small. We conclude that the lizards must have survived the hurricane in the egg stage. This discovery implies that lizard eggs can survive immersion in salt water for some time—in this case, up to 6 h based on estimates of storm-surge duration by locals. We are now testing this experimentally and have found that younger (≤10 days old) eggs immersed in sea water for 3 or 6 h do not differ in viability from controls; experiments on older eggs are underway.

The hurricane left the islands divided into one of two discrete states with respect to *A. sagrei*. Each island had either a substantial number of juvenile *A. sagrei*, possibly enough to 'seed' a new population, or it had zero individuals recorded during at least one time (Fig. 3). Populations of *A. sagrei* on all eight islands of the first state re-attained pre-hurricane levels in about 14 months. One of the four islands of the second state had never contained *A. sagrei* populations (N1), whereas two others (A18, X10) had one, and the fourth (Z3) had two *A. sagrei* at the last census; the individual on X10 and at least one on Z3 were almost certainly natural colonists—those islands are very close to a mainland source.

Which of the two states an island occupied was not random with respect to the presence of the large predator, *L. carinatus*. All six
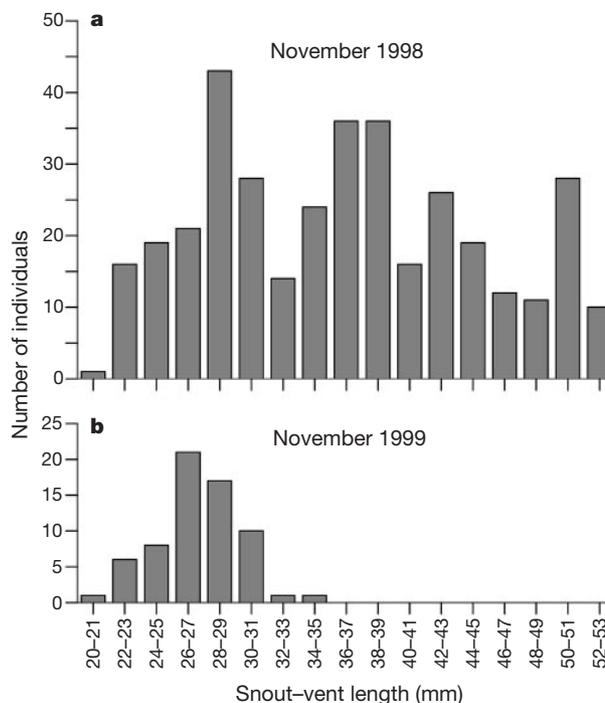

Figure 2 The abundance distribution of *A. sagrei* on all islands combined before (**a**) and after (**b**) hurricane Floyd. The sizes are approximate, that is, they were estimated visually. $N = 360$ (**a**) and 65 (**b**).

islands without the large predator showed the pattern of complete recovery, whereas four of the islands which had *L. carinatus* populations before the hurricane showed the pattern of extinction or extreme population reduction. The overall pattern, four of six populations becoming extinct on predator-introduction islands versus zero of six on control islands, is significant with a Fisher exact test (one-tailed $P = 0.030$).

Although *L. carinatus* had diminished populations of *A. sagrei* to about half the control average by the time of the census immediately preceding the hurricane, population–size rank itself was not a significant predictor of extinction versus survival (Wilcoxon–Mann–Whitney test: one-tailed $P = 0.107$, $n = 12$). Indeed, the presence of the large predator increased the proportional amount by which *A. sagrei* populations were lowered after the hurricane: the percentage drop from the census before the hurricane to the census taken two months afterwards averaged 61.0 for islands without *L. carinatus* and 85.7 for islands with that predator (Median test for difference in percentage decline: one-tailed $P = 0.014$). This unexpected result, although it is not independent of the result for predator introduction versus extinction, provides insight into how predation acts synergistically with disturbance to cause extinction.

To explain it we offer three hypotheses: first, immediate post-hurricane predation by the *L. carinatus* that survived as eggs on some of the islands may have directly reduced *A. sagrei* hatchling numbers; thus the continuing presence of the predator is important. This hypothesis is supported by the fact that the two predator-introduction islands on which *A. sagrei* recovered fully (Z2, Z4) had no *L. carinatus* found after the hurricane; on only one of the other four predator-introduction islands were no *L. carinatus* found. Evidence against this first hypothesis is the size of the *L. carinatus* that survived the hurricane, which were hatchlings themselves and may thus have been less able to feed on prey as large as other lizards.

Second, because of the habitat shift of *A. sagrei*, eggs may have been deposited in less secure places, such as high in trees rather than in rock holes or other more protected sites. This is supported by the extreme habitat shift forced upon *A. sagrei* by the large predator: the higher, thinner perches which *A. sagrei* favoured after the introduction of *L. carinatus* (Fig. 1) probably do not have as many secure sites for depositing eggs. For example, treetops would be potentially more vulnerable to the various forces of the storm: wind, driving rain, high waves and the storm surge itself.

Third, the rate of egg production per female may have been reduced by the large predator. This may also be related to the habitat shift: the unsuitable new surroundings may result in reduced food intake and mating frequency in *A. sagrei* thereby lowering reproductive rate. Although we have no data on mating, food intake should be reflected by body condition (weight relative to length); this was significantly reduced on *L. carinatus* islands in adult males but not in females[11]. Small population-size effects could themselves also contribute to lower reproductive rates; however, percentage reduction was not correlated with population size before the hurricane (Spearman rank correlation $= -0.28$, $P > 0.25$, $n = 12$).

Ecologists have long debated the extent to which communities are shaped by biotic versus physical factors[5,13–18]. For example, do the distribution and abundance of species depend more upon the competitors and/or predators present or upon the vicissitudes of climate? The degree to which one or the other is important to some extent determines the predictability of systems, that is, species interactions often have predictable results whereas climatic events and dispersal during recovery from these events are more stochastic. In the present situation, a highly predictable biological interaction between the larger and smaller lizard species reduced the smaller to a population size, and perhaps reproductive state, whereby an unexpected climatic catastrophe caused its extinction on several islands. The timing of the extinctions was not predictable except in the very

short term, but which islands suffered the extinctions was very predictable. Thus, a compounding of (biotic) predation and (physical) cataclysm basically wiped out a species on four islands where it was a prey species rather than being at the top of its food web, a position it enjoyed on all the islands where it survived. The fact that *A. sagrei* is able to consume a very wide variety of prey allows it to maintain very high chronic densities on islands without predators[19,20] and to recover on those islands as well. The larger predator, *L. carinatus*, also has a very general diet[10], yet because of its size, is unable to exist at nearly as high densities: before the hurricane, *L. carinatus* (even with artificial supplementation) maintained numbers about an order of magnitude lower than those of *A. sagrei*—6.9 versus 54.4 individuals per island. Indeed, *L. carinatus* became extinct on four of its six islands by November 2000.
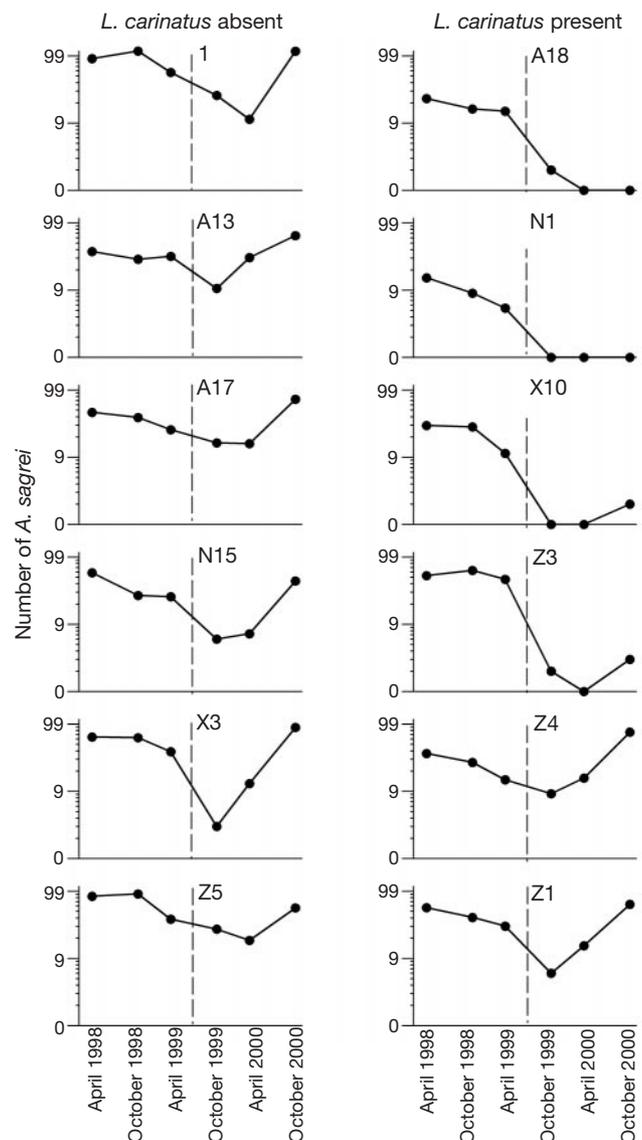

Figure 3 Mortality and recovery or extinction of the lizard *A. sagrei* from hurricane Floyd. Population size is plotted for each census date. Vertical dotted line marks the occurrence of the hurricane. The left column shows control islands, without the large predatory lizard *L. carinatus*. The right column shows islands with the large predator introduced. Islands fall into two patterns: (1) those completely recovering, all of which were permanently without the large predator, plus Z4 and Z1 (both of which lost the large predator as a result of the hurricane); versus (2) islands with extinction or extreme population reduction (N1, A18, X10 and Z3). Three of the latter islands (all but A18) had the large predator at least some of the time after the hurricane.

How widespread is the phenomenology we have been able to demonstrate? The reduction and even extinction of populations by a combination of biotic and physical mortality factors should be quite common. Indeed, we suggested this general mechanism for the extinction of spider species on smaller islands of the same archipelago, but we had no direct evidence[20]. Physical disturbance that is catastrophic, such as that resulting from hurricanes, is itself less common of course, so co-action with a biotic factor such as predation would perforce be even less common; the spider example just given involves more frequent, less catastrophic storms. The unanticipated nature of hurricanes makes even rarer the observations necessary to record their effects; a measure of serendipity is required[21]. But this may change: the gradual increase in sea surface temperatures, perhaps related to climate change[22,23], appears to be contributing to the increase in hurricane frequency. In fact, five of the last six years have had a greater than average number of Category III or more severe hurricanes (see http://weather.unisys.com/hurricane/atlantic/index.html); one must go back to 1969 to accumulate another five years that are above average. Thus, the direct effects of climatic catastrophes as well as interactive effects with biotic factors, some producing extinctions, may be on the rise. Conservation biology might profit from consideration of both kinds of effects in analysing extinction risk. □

Methods

Study site and subject species

The study islands ranged in vegetated area from 137 to 270 m^2 ($\bar{x} = 191.0$). All were covered with fairly closely spaced shrubs and trees seldom exceeding 2 m. All were located in an approximately 7 × 2 km area that encompassed several protected 'creek' waterways fanning out from Buckaroon bay and Snake cay, Great Abaco, the Bahamas.

The manipulated species was the lizard *Leiocephalus carinatus armouri*, a subspecies native to the Little Bahama bank[24]; it is one of the larger forms of the species[14] (maximum snout–vent length: male, 107 mm; female, 97 mm). The subject lizard species *A. sagrei* is substantially smaller (maximum snout–vent length: male, 57 mm; female, 44 mm). *Leiocephalus carinatus* prefers substantially lower perches than does *A. sagrei*[25], and it is most frequently found on the ground. Although it is thus more arboreal than *L. carinatus*, *A. sagrei* in more diverse lizard communities perches lower than other *Anolis* lizards[26]

Experimental protocol

To select islands for introductions, we first (in 1996) stratified the 12 islands with populations of *A. sagrei* into six pairs according to area, vegetation structure and number of *A. sagrei*. One of the islands was naturally colonized in the ensuing year (see above); we randomly chose one of each of the remaining five pairs of islands for the introduction of *L. carinatus*. Throughout the experiment, we attempted to maintain each *L. carinatus* population at five or more individuals by further introductions when necessary. After 1.5 yr, the populations stabilized on all islands and we did not have to add more.

Lizard censuses

Lizard numbers were estimated using the multiway-contingency-table procedure[27,28]; three censuses are done on each of three different days, during which lizards are marked with a census-specific colour of water-soluble latex paint administered with Indico long-distance spraying devices. We used a multivariate-contingency-table method to fit the data to each of eight models, distinguished by which interactions (associations between the three censuses), if any, are included. The simplest of the models fitting the data adequately was selected and the estimate provided by that model was used. A Pascal program doing the fits was kindly provided by J. Roughgarden. Occasionally the program ran no model on the data; then we used the average of the possible pairwise Lincoln estimates (further details in ref. 11). We performed Fisher exact and median tests with SAS software; and used the Wilcoxon–Mann–Whitney test from ref. 29.

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Essential role for Gab2 in the allergic response

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Dos/Gab family scaffolding adapters (Dos, Gab1, Gab2) bind several signal relay molecules, including the protein-tyrosine phosphatase Shp-2 and phosphatidylinositol-3-OH kinase (PI(3)K); they are also implicated in growth factor, cytokine and antigen receptor signal transduction[1]. Mice lacking Gab1 die during embryogenesis and show defective responses to several stimuli[2,3]. Here we report that Gab2$^{-/-}$ mice are viable and generally healthy; however, the response (for example, degranulation and cytokine gene expression) of Gab2$^{-/-}$ mast cells to stimulation of the high affinity immunoglobulin-ε (IgE) receptor FcεRI is defective. Accordingly, allergic reactions such as passive