

Impact of an extreme climatic event on community assembly

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Extreme climatic events are predicted to increase in frequency and magnitude, but their ecological impacts are poorly understood. Such events are large, infrequent, stochastic perturbations that can change the outcome of entrained ecological processes. Here we show how an extreme flood event affected a desert rodent community that has been monitored for 30 years. The flood (i) caused catastrophic, species-specific mortality; (ii) eliminated the incumbency advantage of previously dominant species; (iii) reset long-term population and community trends; (iv) interacted with competitive and metapopulation dynamics; and (v) resulted in rapid, wholesale reorganization of the community. This and a previous extreme rainfall event were punctuational perturbations—they caused large, rapid population- and community-level changes that were superimposed on a background of more gradual trends driven by climate and vegetation change. Captured by chance through long-term monitoring, the impacts of such large, infrequent events provide unique insights into the processes that structure ecological communities.

desert rodents | incumbency advantage | punctuational dynamics

As global climate change scenarios consistently forecast, recent years have witnessed increases in the intensity and frequency of extreme climatic events, including greater variability in precipitation in the southwestern United States (1–4). These events have raised questions about their ecological impacts on the structure and dynamics of populations and communities. Changing climate has caused short-term changes in primary productivity and abundances of individual species (5–8), as well as longer-term shifts in geographic ranges, phenology, and vegetation structure (7–11) and even evolutionary changes (12). Increasing variability of rainfall has been shown to alter the competitive dynamics and species composition of plant communities (13, 14). Still missing, however, is a general perspective on how such large perturbations affect assemblages of diverse kinds of organisms (10, 15–17).

Extreme climatic events, such as floods and droughts, are stochastic perturbations that have the potential to alter the outcomes of entrained population and community processes. The assembly of communities is a dynamic process in which species composition changes as some species, native or exotic, colonize or increase in abundance while other species decrease or go locally extinct (18–20). Although driven in part by deterministic intrinsic interactions, such as competition (21) and predation (22), community assembly is also influenced by stochastic extrinsic perturbations, such as physical disturbances (23), disease epidemics, and colonization of new species (24). Extreme climatic events represent massive, infrequent abiotic perturbations that can differentially affect certain species, thereby altering species composition, resource use, and interactions (10, 14–16). Effects of such perturbations on the long-term dynamics of communities are neither well documented nor well understood, most likely as a result of their rarity and stochasticity. By their very nature, infrequent unpredictable phenomena will never be subject to statistical inference that requires replication, control of variables, or large sample sizes. Nevertheless, impacts of these events can provide valuable insights into the

processes—extrinsic and intrinsic, biotic and abiotic, deterministic and stochastic—that structure communities.

Long-term monitoring of community dynamics provides unique opportunities to observe extreme climatic events and to document their ecological impacts (8, 25–27). Since 1977, a community of seed-eating rodents near Portal, AZ, has been censused monthly, and two extreme precipitation events have been documented. The first occurred in 1983 when Tropical Storm Octave brought 129 mm of rain ($\approx 50\%$ of average annual rainfall) over 6 days (25). The second and most recent occurred when a summer thunderstorm dropped 30 mm of rain in < 2 h on August 14, 1999, causing sheet flooding to an average depth of ≈ 35 cm (28). These two events had large, but strikingly different, impacts on the rodent community.

Here we document the immediate and long-term impacts of the 1999 flood and then briefly compare them to the impacts of the 1983 event. The long-term study includes standardized monthly censuses of rodents, which allow us to (i) measure species-specific responses; (ii) compare community composition and dynamics before and after; and (iii) evaluate the effects of both massive perturbations and background processes, both stochastic and deterministic phenomena.

The Setting: Pre-Flood Community Dynamics

Since 1977, the seed-eating rodent community at Portal has experienced gradual yet profound changes due to climate and vegetation change (29, 30). Higher-than-average winter precipitation increased shrub cover 3-fold (29). Total abundance of seed-eating rodents fluctuated in the short term and increased significantly over the three decades (Fig. 1) (31). Major changes in rodent species composition also occurred (30). Previously dominant, large-bodied kangaroo rats declined; *Dipodomys spectabilis*, formerly the second most abundant species and a keystone species of desert grasslands, went locally extinct in 1994 (25). These declines were compensated by large increases in smaller pocket mice characteristic of shrub habitat, especially *Chaetodipus penicillatus* and *Chaetodipus baileyi* (31, 32). The latter, a native species previously restricted to shrubbier habitats in the surrounding region, first appeared on the site in 1995 (Fig. 2E) (33). Colonization by *C. baileyi* followed a protracted drought when rodent abundance was well below the long-term average (Fig. 1) (28), and one species, the kangaroo rat *Dipodomys merriami*, comprised $> 80\%$ of the total (Fig. 2A). After colonization in 1995, *C. baileyi* increased near-exponentially (33), but by the time of the 1999 flood it was still a distant third in relative abundance (8%) compared with the kangaroo rats *D. merriami* and *Dipodomys ordii* (56% and 15%, respectively) (Fig. 2).

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tions can have effects on populations that last much longer than would be expected from simple recovery dynamics.

Changing Community Composition. An immediate and long-lasting effect of the above population-level responses was a wholesale reorganization of the rodent community, a permanent shift of unprecedented magnitude to a new community composition dominated by pocket mice and not seen in the 22 years before the flood (Figs. 1 and 2). This community reorganization resulted in the invading species, *C. baileyi*, becoming the most abundant species in 2000, displacing *D. merriami*. *C. penicillatus* became the most abundant species in 2005 and has held that position through June 2007. Previously, another dramatic change in community composition marked the colonization of the site by the pocket mouse *C. baileyi* in 1995 (Fig. 1) after a prolonged period of below-average precipitation (28). The ongoing population increase of this species was accelerated by the flood, and it became the most abundant species <5 years after its arrival. So community structure and dynamics can be reset on a new, relatively stable trajectory by both biotic and abiotic perturbations. One kind of biotic perturbation, seen here, is the invasion of a new species, which can be facilitated by abiotic disturbance. An important process in these dynamics is immigration from the pool of individuals and species in surrounding habitats (the metacommunity). The rapidity of population increases and the low frequencies of reproductive individuals (our unpublished data) indicate that the increases of pocket mice immediately after the flood were due predominantly to immigration.

Comparison to 1983 Flood Event. The third major shift in community composition during the 30-year history of the study occurred in response to another extreme climatic event, the excessive rainfall associated with Tropical Storm Octave in October 1983 (Fig. 1). The nature of this storm and its impact on the rodent community were markedly different from the August 1999 thunderstorm. In contrast to the 2-h thunderstorm, Octave lasted for 6 days. Rather than causing sheet flooding and immediate mortality, the prolonged heavy rainfall saturated the soil to great depth, likely causing spoilage of the seeds stored by rodents in deep granaries (25, 28). The greatest impact was on the largest and second most abundant rodent, the kangaroo rat *D. spectabilis*. Already decreasing gradually in abundance because of vegetation change before the storm, it suffered unprecedented mortality over the ensuing months, the winter and spring of 1983–1984 (25). The effect of Octave was to reset the existing decline, so that *D. spectabilis* never recovered its prestorm abundance and went locally extinct in 1994.

Comparison of these two extreme rainfall events shows both similarities and differences. Both storm events caused massive and highly species-specific mortality of dominant species, which resulted in long-lasting shifts in community composition. The causes of deaths, the time lag between the event and mortality, and the species affected, however, were totally different. The soaking of soil and spoilage of seed stores that caused the gradual die-off in *D. spectabilis*, a larder hoarding species, had no detectable impact on *D. merriami*, whose seed stores in shallow surface caches presumably dried rapidly and were undamaged. So, again, a general message from comparing the two storms is that extreme events can have species-specific impacts, which depend crucially on seemingly idiosyncratic details of biology but can nevertheless set in motion wholesale and long-lasting reorganization of the community.

Intersection of Extrinsic Perturbations and Intrinsic Interactions. The dynamics of the rodent community at Portal can be characterized as continually changing, with relatively gradual long-term trends due to background climate and vegetation change punctuated by wholesale reorganizations initiated by infrequent

extrinsic perturbations (i.e., short-term extreme rainstorms) with massive impacts (25, 29, 30). To understand the impacts of the extrinsic abiotic drivers, it is essential to take account of the intrinsic competitive interactions among the rodent species. Most of the time, the seed-eating rodents at Portal are food-limited, and competition is intense because they share a common resource (34–36). This is evidenced by (i) zero-sum dynamics, such that the collective rate of energy use by all rodent species remained relatively constant over the 30 years (31, 32); and (ii) consistent, positive responses of small species, especially pocket mice, to our kangaroo rat removal experiments (33, 37). From this evidence, we infer that (i) the long-term change in precipitation regime was a gradual perturbation that favored some species to the detriment of others, resulting in gradual compositional change and long-term compensatory dynamics driven by competition for limited resources (32); and (ii) the extreme storms were large perturbations that also differentially impacted species and resulted in community reorganization under the influence of strong competition. However, in the second case, reassembly, driven by either immigration after the localized thunderstorm or reproduction after the spatially extensive tropical storm, was very rapid, and a new relatively stable species composition was established in a matter of months. Although some responses to these different types of perturbations were similar, the resulting compositions of the reassembled communities were very different because of the interaction between the selective mortality and preexisting species composition and environmental conditions.

Overcoming Incumbency Advantage. Reassembly after the flood did not change the identity of the four most abundant species, but it did change the interactions among these species. The long-term increase of *D. merriami* in response to the increase in shrubby vegetation and the decline of its larger competitor, *D. spectabilis*, was reversed (Fig. 2), and the ensuing decline of *D. merriami* allowed pocket mice to increase and ultimately dominate the community. These dynamics indicate that the differential mortality caused by the flood altered the preexisting dominance hierarchy, allowing formerly subordinate species that survived the event to dominate. The best explanation for these changes is that resident individuals and species had an incumbency advantage (38). Such a phenomenon has been documented for territorial individuals within species (39, 40). Here, however, loss of incumbency advantage altered interspecific competitive interactions, with profound, long-lasting effects on community structure. Such an advantage is not surprising in these desert rodents, which have established home ranges, seed stores, and burrow systems, and which rely on acquired knowledge of their territory for food finding and predator avoidance (41). Incumbency facilitates not only defense of the territory by the resident individual, but also inheritance of the home range by an offspring or conspecific upon the death of the resident. Under background conditions the effect of the incumbency advantage was to slow down and stabilize population and community dynamics.

The extreme storm event had a destabilizing effect. By causing wholesale mortality of the dominant resident rodents, the perturbation largely eliminated their incumbency advantage, made competitive interactions more nearly equal, and allowed new individuals of previously subordinate species to colonize and establish territories. The mortality of dominant residents made available the resources that they had stored and defended, and previously subordinate rodents were able to immigrate and increase. The effect of the flood in facilitating immigration of previously rare native species was similar to effects of other perturbations in facilitating colonization of exotic invasive species (24, 38, 42, 43). So, disrupting the incumbency advantage is one way that an extrinsic abiotic

perturbation can interface with intrinsic competitive processes to alter assembly rules and cause wholesale community reorganization. Similar responses have been reported in plant communities in response to fire or grazing (38). Priority effects, a form of incumbency advantage for sessile organisms, are frequently invoked to account for such dynamics (44).

Furthermore, our long-term record of community dynamics on ecological time scales seems to be similar to the long-term fossil record of species dynamics on evolutionary time scales. At Portal, gradual long-term trends were punctuated by mass mortality triggered by two extreme precipitation events. In the fossil record, gradual long-term trends were punctuated by mass extinctions triggered by asteroid impacts or other perturbations (45). And in both cases massive mortality of previously dominant taxa removed their priority effects, allowed rapid increases in some surviving, previously subordinate taxa, and resulted in novel species compositions.

Concluding Remarks. Global warming is predicted to increase the frequency and magnitude of extreme climate and weather events (2, 4). Efforts to document these perturbations and to understand their environmental implications have been hampered by a lack of data, due in large part to a paucity of studies of sufficient duration and intensity (3, 13, 16). Consequently, many of the “extreme events” that have been studied are more frequent and predictable than the two storms documented here. For example, there is a substantial literature on the ecological impacts of the El Niño Southern Oscillation, and in particular on the effects of the high rainfall and severe drought during El Niño and La Niña years, respectively (8). Some of the impacts are similar to those reported here. In coastal Chile, for example, El Niño events resulted in substantial changes in desert rodent community composition, due in large part to immigration from surrounding habitats (46, 47). But other impacts are very different. For example, the main effect of El Niño was prolonged population increases fueled by a pulse of abundant new food resources, whereas the main effect of our severe storms was rapid population decreases due to catastrophic mortality. Moreover, El Niño did not have such a dramatic impact on the rodent community at Portal, where several El Niño events were not followed by increases in abundances (28).

Given the diverse phenomena that have been termed “extreme events,” the relatively small number of such events that have been studied, and the diverse ecological responses that have been documented at population, community, and ecosystem levels (see above), it is premature to make sweeping generalizations. Nevertheless, comparisons between the two extreme storms at Portal, and between them and other weather and climate events reported in the literature, suggest that there may be some emerging common themes. For example, massive differential mortality and resetting of community dynamics also occurred in plant communities in response to extreme drought conditions (16, 17). Mortality caused by a hurricane interacted with intrinsic predator–prey interactions to alter population trends in insular spider and lizard communities (48, 49). The effects of such perturbations would have been very difficult to

predict, but, once documented, they provide invaluable insights into the processes of population dynamics and community assembly. Our study is unique, using intensive long-term sampling to document how extreme climatic events can decimate resident species populations, alter species composition and interspecific interactions, and influence invasion dynamics. These unexpected and important results emphasize the need for additional empirical and theoretical work on the ecological consequences of global climate change.

Methods

In 1977 J.H.B. and colleagues began a long-term study in the Chihuahuan Desert near Portal, AZ. Detailed information on the history of the study, monitoring protocols, experimental design, and previous results can be found in Brown (37). This study is restricted to the granivorous rodent community at the site, comprising eight species before the flood (*D. merriami*, *D. ordii*, *C. baileyi*, *C. penicillatus*, *Perognathus flavus*, *Reithrodontomys megalotis*, *Peromyscus eremicus*, and *Peromyscus maniculatus*). To assess trends over time, we calculated relative abundances of species, averaging monthly capture data over 6-month periods (January–June and July–December). Using relative rather than absolute abundances accounts for variation in total abundance of all species, which fluctuated with resource availability (Fig. 1). Trends in relative abundances before the flood are shown on two time scales: (i) to allow comparisons of long-term population dynamics, we analyzed all data since 1977; and (ii) to better characterize shorter-term trends before the flood and take into account the impact of the newly colonized species, we used only data after the first appearance of *C. baileyi* in 1995. Temporal trends were quantified by using ordinary least squares (OLS) regression. There were significant temporal autocorrelations in the population dynamics, but regressions were used only to describe trends, not to compare statistical significance. Expected abundances for 6-month periods after the flood were calculated by extrapolating the ordinary least squares regression equations; these postflood expected values were then compared with observed values for the corresponding 6-month period using paired *t* tests. Relative abundances were arcsine-transformed ($p' = \arcsin \sqrt{p}$). Percent survivorship of each rodent species was calculated as the percentage of individuals captured in one 6-month period (e.g., January–June 1999, immediately preceding the flood) that were recaptured in subsequent 6-month periods. The background rates of survivorship were calculated as the percentages of all individuals marked from 1978 through 1999 that were recaptured in subsequent 6-month periods. Because these values are simply percentages based on all data, there is only one value per species per 6-month period, and therefore no statistical comparison was performed. We used recapture rate as a surrogate for survivorship, because (i) it is a simple calculation, unburdened by assumptions about trappability, movement, and death; and (ii) the actual fate of each individual not recaptured is unknown and irrelevant to our conclusions, but the rapid, concerted, unprecedented disappearance of large numbers of individuals can only reasonably be attributed to mortality. To quantify changes in community composition through time, we followed Ernest and Brown (32) and used the ED to measure the difference in relative abundances of all species between successive 6-month periods.

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- Gordon HB, Whetton PH, Pittock AB, Fowler AM, Haylock MR (1992) Simulated changes in daily rainfall intensity due to the enhanced greenhouse effect: implications for extreme rainfall events. *Clim Dyn* 8:83–102.
- Easterling DR, et al. (2000) Climate extremes: Observations, modeling, and impacts. *Science* 289:2068–2074.
- Weltzin JF, et al. (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53:941–952.
- Diffenbaugh NS, Pal JS, Trapp RJ, Giorgi F (2005) Fine-scale processes regulate the response of extreme events to global climate change. *Proc Natl Acad Sci USA* 102:15774–15778.
- Polis GA, Hurd SD, Jackson CT, Pinero FS (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* 78:1884–1897.

- Gannon MR, Willig MR (1998) in *Forest Biodiversity in North, Central, and South America and the Caribbean: Research and Monitoring*, eds Dallmeier F, Comisky J (Parthenon, Washington, DC), pp 271–291.
- Holmgren M, Scheffer M, Ezcurra E, Gutierrez JR, Mohren GMJ (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol Evol* 16:89–94.
- Holmgren M, et al. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Front Ecol Environ* 4:87–95.
- Allen CD, Breshears DD (1998) Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation. *Proc Natl Acad Sci USA* 95:14839–14842.
- Parnesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. *Bull Am Meteorol Soc* 81:443–450.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

12. Grant BR, Grant PR (1993) Evolution of Darwin's finches caused by a rare climatic event. *Proc R Soc London Ser B* 251:111–117.
13. Knapp AK, et al. (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205.
14. Chesson P, et al. (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253.
15. Paine RT, Trimble AC (2004) Abrupt community change on a rocky shore: Biological mechanisms contributing to the potential formation of an alternative state. *Ecol Lett* 7:441–445.
16. Miriti MN, Rodriguez-Buritica S, Wright SJ, Howe HF (2007) Episodic death across species of desert shrubs. *Ecology* 88:32–36.
17. Haddad NM, Tilman D, Knops JMH (2002) Long-term oscillations in grassland productivity induced by drought. *Ecol Lett* 5:110–120.
18. Fox BJ (1987) Species assembly and the evolution of community structure. *Evol Ecol* 1:201–213.
19. Tilman D (2004) Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc Natl Acad Sci USA* 101:10854–10861.
20. Zavaleta ES, Hulvey KB (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306:1175–1177.
21. Kelt DA, Taper ML, Meserve PL (1995) Assessing the impact of competition on community assembly: A case-study using small mammals. *Ecology* 76:1283–1296.
22. Stoks R, McPeck MA (2003) Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. *Ecology* 84:1576–1587.
23. Burke MJW, Grime JP (1996) An experimental study of plant community invasibility. *Ecology* 77:776–790.
24. Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176.
25. Valone TJ, Brown JH, Jacobi CL (1995) Catastrophic decline of a desert rodent, *Dipodomys spectabilis*: Insights from a long-term study. *J Mamm* 76:428–436.
26. Marques SC, Azeiteiro UM, Martinho F, Pardal MA (2007) Climate variability and planktonic communities: The effect of an extreme event (severe drought) in a southern European estuary. *Estuar Coast Shelf Sci* 73:725–734.
27. Miriti MN (2007) Twenty years of changes in spatial association and community structure among desert perennials. *Ecology* 88:1177–1190.
28. Brown JH, Ernest SKM (2002) Rain and rodents: Complex dynamics of desert consumers. *Bioscience* 52:979–987.
29. Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proc Natl Acad Sci USA* 94:9729–9733.
30. Thibault KM, White EP, Ernest SKM (2004) Temporal dynamics in the structure and composition of a desert rodent community. *Ecology* 85:2649–2655.
31. White EP, Ernest SKM, Thibault KM (2004) Trade-offs in community properties through time in a desert rodent community. *Am Nat* 164:670–676.
32. Ernest SKM, Brown JH (2001) Homeostasis and compensation: The role of species and resources in ecosystem stability. *Ecology* 82:2118–2132.
33. Ernest SKM, Brown JH (2001) Delayed compensation for missing keystone species by colonization. *Science* 292:101–104.
34. Brown JH, Munger JC (1985) Experimental manipulation of a desert rodent community: Food addition and species removal. *Ecology* 66:1545–1563.
35. Heske EJ, Brown JH, Mistry S (1994) Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* 75:438–445.
36. Valone TJ, Brown JH (1995) Effects of competition, colonization, and extinction on rodent species diversity. *Science* 267:880–883.
37. Brown JH (1998) in *Issues and Perspectives in Experimental Ecology*, eds Resetarits WL, Jr, Bernardo J (Oxford Univ Press, Oxford), pp 71–95.
38. Corbin JD, D'Antonio CM (2004) Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology* 85:1273–1283.
39. Davies NB (1978) Territorial defence in speckled wood butterfly (*Pararge aegeria*): Resident always wins. *Anim Behav* 26:138–147.
40. Takeuchi T (2006) Matter of size or matter of residency experience? Territorial contest in a green hairstreak, *Chrysophrys smaragdinus* (Lepidoptera: Lycaenidae). *Ethology* 112:293–299.
41. Genoways HH, Brown JH, eds (1993) *Biology of the Heteromyidae* (Am Soc Mammalogists, Lawrence, KS), Special Publication No. 10.
42. Moulton MP, Pimm SL (1986) in *Community Ecology*, eds Diamond J, Case TJ (Harper and Row, New York), pp 80–97.
43. Sher AA, Hyatt LA (1999) The disturbed resource-flux invasion matrix: A new framework for patterns of plant invasion. *Biol Inv* 1:107–114.
44. Paine RT (1977) in *The Changing Scenes in Natural Sciences*, ed Goulden CE (Special Publication 12, Academy of Natural Sciences), pp 245–270.
45. Jablonski D, Sepkoski JJ (1996) Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–1378.
46. Meserve PL, Milstead WB, Gutierrez JR (2001) Results of a food addition experiment in a north-central Chile small mammal assemblage: Evidence for the role of “bottom-up” factors. *Oikos* 94:548–556.
47. Meserve PL, Kelt DA, Milstead WB, Gutierrez JR (2003) Thirteen years of shifting top-down and bottom-up control. *Bioscience* 53:633–646.
48. Schoener TW, Spiller DA, Losos JB (2001) Predators increase the risk of catastrophic extinction of prey populations. *Nature* 412:183–186.
49. Schoener TW, Spiller DA (2006) Nonsynchronous recovery of community characteristics in island spiders after a catastrophic hurricane. *Proc Natl Acad Sci USA* 103:2220–2225.