



The Introduced Hawaiian Avifauna Reconsidered: Evidence for Self-Organized Criticality?

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Over the last century, many bird species have been introduced into the Hawaiian islands. The data indicate a scenario in which island communities build up to a critical number of species, above which avalanches of extinction occur. Plotting the distribution of extinction event sizes approximates a power-law in accordance with the notion of a self-organized critical system. The lengths of time between introduction and extinction for different species also exhibit power-law scaling. These results suggest that ecological communities are not characterized by a well defined equilibrium, but rather by a detailed balance which is minimally stable to perturbations such that the introduction of species can trigger extinction cascades.

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Introduction

In a series of papers, Moulton & Pimm (1983), Simberloff & Boecklen (1991) and Moulton (1993) considered the role of competition in structuring communities of birds introduced to the Hawaiian Islands. The primary argument in this debate has been whether extinction rate increases nonlinearly with an increasing number of species. The logic of this argument stems from the fact that the number of potential interactions between species increases proportional to the number of species squared. Thus, a quadratic relationship between extinction rate and species richness implies that competition is forcing some species to extinction. Moulton & Pimm (1983) found that for six islands in the Hawaiian Archipelago, a quadratic function provided a better fit to the data than did a linear model. However, Simberloff & Boecklen (1991) disputed the results

based on non-independence and other problems with the data. When a repeated-measures model was used, the data were insufficient to support a quadratic fit over a linear model. Moulton (1993) recently responded to these criticisms, reasserting that the data support competition.

In the present paper, we offer an alternative interpretation of the Hawaii data. Although our results have implications for the question of competition, we are more concerned with the kind of dynamical system that results from a process of community assembly. In particular, we show that several patterns in the data support Bak *et al.*'s (1988) theory of self-organizing criticality. We make three observations that show that the colonization-extinction record of the introduced Hawaiian avifauna is consistent with self-organized criticality: (1) a discontinuity in the plot of extinction rate vs. species richness suggesting a critical number of species, above which cascades of extinction occur, (2) an approximate $1/f$ or power-law distribution of extinction event sizes, and (3) a power-law distribution of species waiting times to extinction.

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Self-organized Criticality

Nature appears to be intermittent, i.e., it is characterized by large fluctuations interspersed among periods of relative stasis (Bak, 1991; Holling, 1992). At the broadest evolutionary scales, adaptive radiations appear, in some cases, to occur in short bursts of evolutionary activity, a phenomenon known as punctuated equilibrium (Gould & Eldredge, 1977; Eldredge & Gould, 1988). Raup (1982) has shown that the fossil record is marked by intermittent mass extinction events. He noted that “[e]xtinction may be episodic at all scales, with relatively long periods of stability alternating with short-lived extinction events.” (Raup, 1986, p. 1528). Meteorite impacts have played a role in extinction events (Alvarez *et al.*, 1980). However, unless one is willing to accept that all extinction events are of extraterrestrial origin, we are confronted with the question: is intermittency intrinsic to the organization of ecological communities? If ecological communities are generally characterized by intermittent extinctions, then we should observe patterns similar to those described for the fossil record in small, locally interacting species assemblages.

A model to explain the origin of intermittent fluctuations in non-equilibrium systems has been given by Bak *et al.* (1987, 1988). Bak and co-workers proposed that many complex systems naturally evolve to a critical state defined by the spontaneous emergence of intermittent fluctuations across a broad range of spatial and temporal scales without any “fine tuning” necessary from outside the system. They have termed this phenomenon “self-organized criticality” (SOC). A metaphor for SOC is a pile of sand to which sand grains are continually added (Bak *et al.*, 1987, 1988). Initially when the pile is flat there is relatively little interaction among different regions of the pile and adding a single grain will only affect a few other grains nearby. The system is in a subcritical state. As the pile increases in height, avalanches of grains spill down the sides such that adding a single grain can initiate a cascade affecting many other grains. Eventually, the pile reaches a critical state and essentially does not get any steeper. The critical state is defined by a stationary statistical distribution of avalanches which propagate across all spatial and temporal scales (only limited by the finite size of the pile). Alternatively, the pile could be started in a supercritical state by forming a vertical cylinder of sand. A supercritical pile is highly unstable and is expected to collapse down to a critical state as grains are added. Thus, one can think of the critical state as an attractor for the dynamics of the pile.

For a critical system, the distribution of fluctuation sizes is described by a power-law of the form

$$D(s) \approx s^{-\alpha} \quad (1)$$

where s is the size of an “avalanche” and $D(s)$ is the frequency of its occurrence. The negative exponent of the distribution leads to many small events or fluctuations punctuated by progressively rarer large events, hence the notion of intermittency.

To estimate α , the system in question is observed over a period of time and the frequency of events of size s is recorded. In the sandpile example, the events are avalanches of sand grains, and the size of an event is the number of grains in a particular avalanche. Frequency is estimated as the number of events of size s divided by the total number of events. The slope of the data on a log-log plot gives the estimate of α . For large systems and in simulation models, the estimate of α can often be taken by hand; for smaller systems, regression can be used. Linear regression on the log-transformed data is preferable to nonlinear regression on the raw data because the residual error will be distributed as a quadratic and the minimum error is guaranteed. This is not the case with nonlinear regression.

Critical fluctuations are often referred to as obeying a “ $1/f$ ” distribution, i.e., the size of an event decreases as the inverse of the frequency with which it occurs. This is simply a restatement of the expression given in eqn. (1). Since $D(s) = f$, from eqn. (1) we have $s = 1/f^{1/\alpha}$. Notice that for the $1/f$ distribution, the scaling exponent is the inverse of that found for the event-size frequency distribution [eqn. (1)].

Self-organized criticality occurs in systems that build up stress and then release the stress in intermittent pulses. An example is stress that builds up in the earth’s crust and is released in earthquakes (Feder & Feder, 1991). This is described by the well-known Gutenberg–Richter law of geophysics that states that the number of earthquakes N with energy greater than E is given by

$$N(E_0 > E) \approx E^{-B} \quad (2)$$

where B is the scaling exponent describing the distribution (Olami *et al.*, 1992). There are numerous other examples in the physical sciences (Poliakov & Herrmann, 1994; Cannelli *et al.*, 1994; Noever & Cronise, 1994; Wang & Shi, 1994). Recently, SOC was evoked to explain patterns of tree-fall gap formation in tropical forests (Solé & Manrubia, 1995).

The “avalanches” of extinction observed by Raup may also be indicative of a self-organized critical state (Kauffman & Johnsen, 1991; Flyvbjerg *et al.*, 1993;

Bak & Sneppen, 1993). Kauffman & Johnsen (1991) considered interacting fitness landscapes of coevolving species and showed that such a system could lead to the complex dynamics associated with SOC. Distributions of extinction event sizes in Kauffman & Johnsen's model agreed qualitatively with the distributions found in Raup's (1982) data (Kauffman & Johnsen, 1991). In coevolutionary models, the dynamics are generated principally by species interactions as opposed to transfers of momentum in physical systems. However, it is a key concept in SOC that the dynamics are largely independent of the components comprising the system. Thus, from the standpoint of self-organization, it does not matter whether we are concerned with faulting in the earth's crust, the interactions among species in an assemblage, or the dynamics of sand piles. The macroscopic behavior of critical systems all obey the same dynamical distributions. In the case of coevolving species, exact analytical solutions have been given, demonstrating that extinction cascades following the distributions in eqns (1) and (2) can emerge spontaneously in simple models of coevolution (Flyvbjerg *et al.*, 1993; de Boer *et al.*, 1994). We believe that these results may also apply to a process of community assembly occurring over shorter timescales.

Extinction Dynamics in the Hawaiian Islands

Moulton & Pimm (1983) have described an extensive record of avian species (Columbiformes and Passeriformes) introductions and extinctions for the Hawaiian Islands [later expanded by Simberloff & Boecklen (1991)]. The introductions were all assumed to be intentional releases by human settlers, although in some cases, birds may have spread to other islands via natural dispersal. The data cover a period from 1850 to 1984 and include dates of colonization and (where appropriate) extinction for 69 species of birds introduced to the islands of Oahu, Kauai, Maui, Hawaii, Molokai, and Lanai. Because the chronology was assembled from literature citations and historical accounts, it was difficult to gauge the overall accuracy of the data. Both Simberloff & Boecklen (1991) and Moulton (1993) have raised questions about the accuracy of some records in the data. Nonetheless, the introduction and extinction record for introduced Hawaiian birds is perhaps the best data available to study the assembly of ecological communities at a mesoscale: it is one of the few data sets for which approximate dates of both introduction and extinction are available for a large number of species.

The record of introductions and extinctions in the Hawaiian islands is unique in that it chronicles the complete assembly of a community starting from a nearly "empty" species assemblage. Native Hawaiian birds were driven extinct by humans, initially by Polynesian settlers and later by immigrants from North America. A principle culprit in the decline of native birds has been clearing of land for agriculture and human settlement. Native Hawaiian birds do persist in undisturbed highland habitats; however, the non-native species were introduced and persist in disturbed lowland habitats and interact little with native species (Moulton & Pimm, 1983). Thus, the confounding effect of interactions among native and introduced species was not present in the data. Furthermore, clearing of land during the period of introductions and extinctions has, if anything, increased the area of suitable habitat available to the introduced species. The record of extinctions is therefore unlikely to be the result of changes in available habitat.

Of the 69 bird species introduced to the Hawaiian Archipelago between 1850 and 1984, 35 became extinct. Over the first 70 years, the system gradually accumulated species with no extinction. After roughly eight species had been successfully introduced, numerous extinction events occurred with extinction rate generally increasing as more species were added (although there are "windows" with zero extinction rate above eight species—Fig. 1).

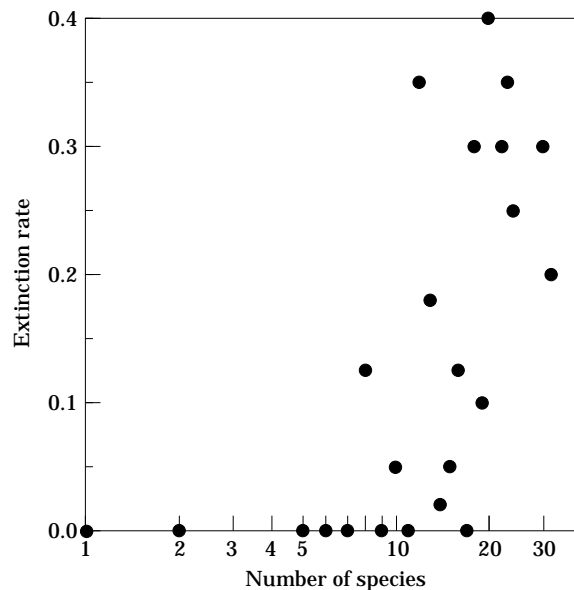


FIG. 1. Extinction rate of introduced Hawaiian avifauna vs the number of introduced bird species. Extinction rate was taken as number of extinctions per species per year measured over 10 year intervals. The data for Figs 1–3 were taken from Simberloff & Boecklen (1991).

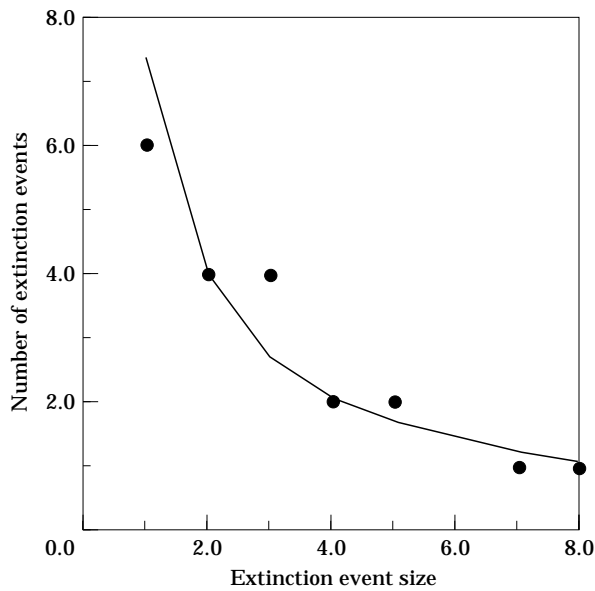


FIG. 2. Distribution of extinction event sizes of the introduced Hawaiian avifauna. The trend line, $N(s) = s^{-0.91}$, is a least squares regression of the log-transformed data ($r^2 = 0.90$, $p = 0.002$).

Because of the limited number of extinction records and the possible interaction among islands due to dispersal, we pooled the data across all islands. If the islands were independent, pooling the data would mask some of the variability among islands. Extinction rate vs. number of species for the pooled data is plotted in Fig. 1. We note that the relatively sharp transition from zero extinction rate to a positive extinction rate is suggestive of a transition from a subcritical system to a critical system. Such patterns are associated with dynamical phase transitions and criticality (Goldenfeld, 1992). Presumably, there also exists a supercritical state at a higher species richness which would be characterized by a rapid collapse to a lower number of species.

It is also worth noting that fitting a continuous function through these data as was done by Moulton & Pimm (1983) may be inappropriate because functions describing critical transitions are generally discontinuous or diverge at higher derivatives (Goldenfeld, 1992). This might explain why Simberloff & Boecklen (1991) found negative extinction rates at low species richness when fitting the data. However, the pattern strongly implies nonlinearity, giving support to the argument of Moulton & Pimm (1983) that nonlinear species interactions structures these assemblages.

The distribution of extinction event sizes for these data exhibit intermittency (i.e., many small and a few large) in concordance with Raup (1982). Decades in which only a single species became extinct were more

numerous than decades in which greater than five species became extinct (Fig. 2). The data represent 59 individual extinction that occurred on six islands in the Hawaiian archipelago. Extinction event size was defined as the number of species reaching extinction during a given decade on a given island. Treating each island separately, there were 20 island-decades between 1920 to 1990 during which species became extinct. The distribution function of extinction events approximates a power-law with an exponent of -0.91 , suggesting critical scaling. The size of extinction cascades therefore scales as $1 = f^{1.09}$ where f is frequency. An approximate randomization test (Noreen, 1989) was used to test the null hypothesis that extinction event size was not related to frequency. The probability that the observed correlation between size and frequency was due to chance was $p = 0.002$. (Of 10000 randomizations, 15 resulted in a correlation greater than or equal to the observed correlation.)

Moulton & Pimm (1983) cited a number of reasons why exogenous perturbations were unlikely as the cause of these extinctions. Although we cannot rule out human disturbance or climatic variability in precipitating extinction cascades, the presence of minor external disturbances would not contradict our basic premise that the interaction among species leads to a critical system that is susceptible to even minor perturbations. We envision a scenario in which interaction “stress” builds up among species occupying localized regions of niche space (i.e., species with similar phenotypic traits) which when reaching a threshold is released in a cascade of extinction.

Another indicator of critical dynamics is a power-law distribution of lifetimes (de Boer *et al.*, 1994). Waiting times to extinction for introduced Hawaiian birds exhibit a power-law distribution with most species persisting only a few years and a few species persisting >60 years before going extinct (Fig. 3). A null model for extinction which is independent of any species interactions is a simple uniform probability of extinction for each species in each time period. This would lead to an exponential distribution of waiting times. However, an exponential model explained less of the variation ($r^2 = 0.56$) than did a power-law ($r^2 = 0.81$). Using an approximate randomization test, the probability that the observed power-law relationship between persistence-time and frequency was due to chance was $p = 0.023$.

These results would also seem to have important implications for the “all-or-none” pattern of extinction forwarded by Simberloff & Boecklen (1991). If some introduced species are poor colonizers, and therefore became extinct independent of interaction

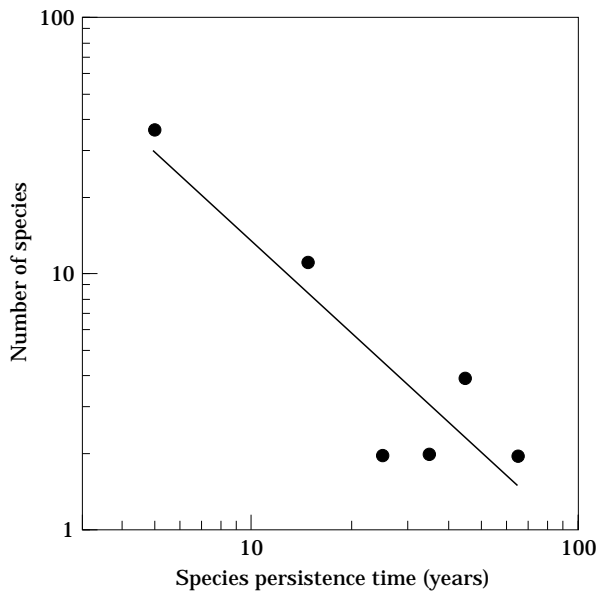


FIG. 3. Distribution of waiting times to extinction for 59 birds species that became extinct between 1920 and 1990 on six Hawaiian islands. Waiting time to extinction is the number of years between introduction and extinction for a given species. The trend line, $N(t) = t^{-1.16}$, was fitted via regression to the log-transformed data ($r^2 = 0.81$, $p = 0.023$).

with other species, then we would expect a rapid, exponential decay in the distribution of persistence times. This is not the case. Instead, the power-law distribution of waiting times suggests a system which is “episodic at all scales”. This is in fact central to the notion of criticality. Critical systems are defined by self-similar or “fractal” dynamics such that any small portion of the system, when viewed at a fine scale, exhibits the same statistical distributions observed for the whole system at a larger scale. Thus, the critical distributions we have described for the introduced Hawaiian birds is consistent with the global scale intermittency described by Raup (1982).

Discussion

Although self-organized criticality describes a particular statistical distribution of events (i.e., extinctions, avalanches, earthquakes), it does not dictate a particular mechanism leading to extinctions. We cannot statistically test hypotheses regarding the cause of the Hawaii extinctions with the current data; however, we can outline some possible scenarios.

The increase in extinction rate above a critical number observed in Fig. 1 suggests that the development of the species assemblage is structured by conflicting constraints. In the case of the sandpile model, the constraints are gravity which acts to lower

the height of the pile and addition of sand grains which raises the height of the pile. The structure of the pile emerges from the interaction of these forces. It is important to realize that, although gravity acts uniformly on all grains in the pile, the probability of an avalanche occurring is not spatially uniform across the pile. Some areas of the pile will have steeper slopes and thus, a higher probability of sliding. Each avalanche changes the spatial pattern of slopes and thereby affects the size of subsequent avalanches, which in turn determine the structure of the pile yet again. It is this pattern of long range correlations among avalanches that is key to understanding SOC.

What constraints then act on the structure and dynamics of an ecological assemblage? In the case of the introduced Hawaiian avifauna, the community structure is the result of introductions that increase the number of species and extinctions which lower the number of species, resulting in a dynamic balance as in the sand pile. The mechanism behind introductions is obvious, but the cause of the extinctions is less clear. A candidate mechanism for extinction is competition among species. If competition is a driving force in structuring the community, then the important dynamics would be observed in the niche space occupied by different species. Competitive pressure would be expected to be high in regions of niche space where species were densely packed, as would happen, for example, when a number of bird species shared the same food resource or nesting requirements. It is possible that, like steep regions of the sand pile, species occupying dense regions of niche space are subject to higher extinction probabilities. The loss of species would change the distribution of species in niche space and, in turn, change the probabilities of future extinctions, much like the dynamics of the sand pile model.

Mechanisms other than competition could also cause extinction. One possibility is human alteration of habitat. Human intervention seems unlikely as a cause of the extinctions because the amount of disturbed habitat into which the birds were introduced has increased during the past century (Moulton & Pimm, 1983). Changes in climate may have also caused extinctions in the Hawaiian Islands. For example, periodic droughts leading to reduced insect populations and fruiting failure could have caused extinctions via starvation, particularly in small bird populations. Typhoons or other severe weather events may also have caused extinctions by direct mortality or habitat destruction. Human activity and climatic factors are both external causes of extinction, i.e., they do not depend on the dynamics of species assemblage. If Hawaiian bird extinctions were caused

solely by external influences, then no appeal to self-organization is necessary.

The presence of external driving forces does not rule out SOC, but raises an important point if SOC is to be applied to many different systems and levels of organization. Self-organized criticality has been posited as governing the dynamics of all "dissipative systems" [i.e., systems through which energy flows; Bak *et al.* (1988), Nicolis & Prigogine (1989)]. If true, this would imply a situation in which essentially any system chosen for study would itself be embedded in a larger critical system. For example, the intensity of ENSO (El Niño/Southern Oscillation) events, in which prevailing ocean currents change direction altering weather patterns throughout the Pacific Basin, appear to follow a critical scaling law (B. Milne, personal communication). The ENSO events could precipitate extinctions in the areas affected (including the Hawaiian Islands). However, the presence of external fluctuations does not rule out SOC as an explanation for the patterns of extinctions observed: a critical system can itself be embedded in a large critical system. The dynamics of hierarchically coupled critical systems remains an open area of research for those developing a theory of self-organizing systems and has implications for the development of hierarchy theory in ecology (Allen & Starr, 1982).

A possible mechanism internal to the system and involving species interactions, but not competition or trophic relations, is disease. Disease and pest outbreaks exhibit intermittent bursts of activity (e.g., Ludwig *et al.*, 1978) although these patterns may not be explicitly linked to SOC. Avian malaria affects many bird communities throughout the world and is likely to be found in Hawaiian birds (May, 1995). Periodic, disease-induced mortality may have reduced some bird populations to the point of extinction. In this case, critical dynamics could emerge from the spreading of the disease and inhibitory feedbacks from either mortality or, if an individual survives, post-infection immunity. While SOC has not been applied to epidemiological models, structurally similar models of forest fires exhibit SOC (Chen *et al.*, 1990; Loreto *et al.*, 1995).

Loss of stability due to trophic and other interactions is another possible mechanism for extinction. Numerous studies of species interaction webs have shown that as more species are introduced to a community the assemblage becomes harder to invade (Post & Pimm, 1983; Drake, 1988, 1991; Pimm, 1991) and less stable (Gardner & Ashby, 1970; May, 1973; Pimm, 1982; Cohen & Newman, 1988; Hastings 1988). Cohen *et al.* (1990) have identified classes of Lotka–Volterra food web models which do

not become unstable as the number of species increases. However, their results apply only in the limit of an infinite number of species and do not explicitly include resource or space limitations. Simulation results that explicitly incorporate space and spatial limitations support the assertion that communities become unstable as species are added and that instability can lead to extinction cascades (T. Keitt, in preparation). It is possible that SOC arises in ecological communities through a process of assembly in which the ecosystem accumulates species until reaching the frontier of stability and then fluctuating around that boundary.

Conclusion

Our analyses of the introduced Hawaiian avifauna suggest that ecological communities assemble to a critical dynamical regime characterized by power-law distributions of extinction events and species persistence times. Critical dynamics have important implications for how we view ecosystems. Traditionally, extinction has been thought to be the result of individual species traits, more-or-less deterministic species interactions, or large-scale disturbance. Instead, SOC suggests a dynamical view of extinction where even small perturbations can precipitate extinction cascades. Extinction events may represent fluctuations in a non-equilibrium dynamical system and have little to do with the traits of individual species. Species in complex communities may in fact be analogous to grains in a sandpile. The fate of a particular grain depends little on its particular shape, but is critically influenced by the overall structure of the pile. Similarly, persistence of species in an assemblage may be largely determined by the "ghost of fluctuations past" which structure the community. We hope that this work will stimulate thinking about complex ecological dynamics and macro-scale explanations for the patterns we observe in ecological systems.

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