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Universal Power Laws Govern Intermittent Rarity in Communities of Interacting Species

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Abstract

The temporal dynamics of many natural populations involve intermittent rarity, that is, the alternation, over variable periods of time, of phases of extremely low abundance, and short outbreaks. In this paper we show that intermittent rarity can arise in simple community models as a result of competitive interactions within and between species. Intermittently rare species are typified as weak invaders in fluctuating communities. Although the dynamics of intermittent rarity are highly irregular, the distribution of time spent in phases of rarity ('rarity times') involves strong regularity. Specifically, intermittent rarity is governed by a well-defined power law. The scaling exponent ($-3/2$) is a universal feature of intermittent rarity: it does not depend on species demographic parameters; it is insensitive to environmental stochasticity; and the same exponent is found in very different models of nonstructured populations. The distribution of rarity times implies that the dynamics of rarity have no characteristic timescale. Yet in practice the universal scaling law offers a general form of prediction in which one can calculate the frequency of occurrence of rarity phases of any given duration. Data on marine fish communities support the prediction of a $-3/2$ power law underlying the dynamics of intermittently rare species. The scale-free dynamics reported here place intermittent rarity in the same class as the critical states of other nonlinear dynamical systems in the physical sciences. At a critical state, general laws govern the systems' dynamics irrespective to the specific details of the interactions between constituents.

Key phrases: Community persistence and mutual invasibility; Intermittent rarity resulting from interspecific competition; Intermittent rarity and weak invasibility; Intermittent rarity and chaos; Statistics of the dynamics of intermittently rare species; Power laws governing intermittent rarity; Universal scaling of rarity times; Examples of models showing intermittent rarity: the Gatto model, the Franke-Yakubu model and the Hochberg-Hawkins model.

Key words: community dynamics, invasibility, competition, chaos, intermittent rarity, power law, universal scaling, criticality.

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Universal Power Laws Govern Intermittent Rarity in Communities of Interacting Species

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Introduction

Understanding the determinants of variability in species abundance is a central issue in ecology. In the context of population management and conservation, the temporal dynamics of rare species pose a difficult puzzle. Many rare species are thought to be on a trajectory to extinction (e.g., Schonewald-Cox and Buechner 1991). Although the destiny of any species is certainly extinction, the relationship between rarity and persistence on the ecological timescale is far from clear (Gaston 1994). Perhaps the most important question one can ask about the temporal dimension of rarity is whether those species which we presently regard as rare have also been so in the past and are likely to be so in the future. There is indeed ample evidence that some animal species persist through intermittent rarity, that is, by alternating long periods of very low abundance and short outbreaks in a seemingly unpredictable way (Vandermeer 1982, Hanski 1985, Rosenzweig and Molino 1997). The population dynamics of pathogens or pests offer examples of such intermittent dynamics, with epidemics being usually regarded as a large positive fluctuation away from the average endemic level (Anderson and May 1992). Likewise, commercial fisheries have to deal with the alternation of periods of resource commonness and periods of scarcity of variable duration, during which some of the exploited species are virtually absent from the catches (May 1984, Rothschild 1986).

Traditional explanations of rarity involve low species' carrying capacity, or alternative stable population states due to « natural enemies » (e.g., Southwood and Comins 1976) or metapopulation structure (Hanski 1985). None of these theories can explain the alternation of long periods of rarity and short bursts of abundance without resorting to external factors: artificial release of control by competitors, predators or pathogens; influx of immigrants; and/or seasonal forcing (Olsen and Schaffer 1990, Royama 1992). More recently, however, Vandermeer (1993) investigated the dynamics of a community of two predators and two preys, showing that the species may experience long periods of rarity interspersed with population flushes if the predators demonstrate asymmetric preferences for their preys. The duration of rarity phases seems unpredictable. This dynamical behavior develops as the overlap of predators' diets increases, near to the point where the four-species community can no longer be sustained and one prey goes extinct.

Although the elementary unit of ecological communities may be the predator-prey connection as envisaged by Vandermeer (1993), a prevailing view has long been that « the explanation of rarity must lie in an evaluation of the competitive competency of species » (Griggs 1940). In this paper we consider simple cases of a general community model (Warner and Chesson 1985) to investigate the occurrence of intermittent rarity among species that compete for a common limiting resource. Continuing from Vandermeer's main findings, we ask under which conditions intermittent rarity can develop among competing species, and whether beyond the apparent irregularity of rarity dynamics noticed by Vandermeer (1993), there are underlying patterns which may be amenable to predictions and recognised in time series of population data.

Empirical Evidence for Intermittent Rarity

The extent to which rare species remain rare in time (and in space) is a pivotal question in community biology (Rahel 1990, Gaston 1997). However, the analysis of temporal rarity dynamics is usually hampered by the short series of population

abundance data. A remarkable exception is provided by the Pacific sardine *Sardinops caerulea* for which subfossil deposits of scales have generated estimates of population size over the past two millennia—a timescale seldomly accessible to ecologists (Soutar and Isaacs 1974, Baumgartner et al. 1992). The data extracted from marine petroleum core show (Fig. 1A) that in over 55% of the decades from the year 160, the sardine was so rare as to be virtually absent from core samples in the Santa Barbara basin; every so often, however, it explodes (Soutar and Isaacs 1974). Other cores in the same and another basin produced similar fluctuations, peaking and declining simultaneously. Despite substantial efforts directed towards the elucidation of the Pacific sardine dynamics, the intermittent and erratic phases of extreme rarity observed in that species remain an ecological enigma (Rosenzweig and Molino 1997).

Following the pioneering research of Soutar and Isaacs (1974), DeVries and Pearcy (1982) have used fish debris preserved in partly laminated marine sediments on the upper continental slope off Peru to reconstruct a history of Holocene fishes, mainly anchovies, sardines and hakes. They have shown that the anchoveta *Engraulis ringens* has usually dominated the pelagic fish community through historical time. In contrast, sardines *Sardinops sagax* occurred erratically and were often so rare that they were not represented in the fish scale record (Fig. 1B). The abundance pattern so obtained over 12,000 years (Fig. 1B) is qualitatively similar to the dynamics during the past 2,000 years (Fig. 1A).

Similar patterns of quasi-extinction during periods much longer than the duration of a species life cycle followed by quick resurgences to high abundance levels have also been observed in the Japanese sardine *Sardinops melanisticta* (Kondô 1987, Cury 1988). Yearly data recorded from the beginning of this century show that Japanese sardines remained at extremely low density till ca. 1925 and experienced another rarity phase between 1945 and 1975 (Kondô 1987). On a longer timescale, Tsuboi (1984) has documented six periods since the early seventeenth century during which the species was common. Rarity phases appear highly variable in their duration: from 20 to 100 years.

Well-documented examples in terrestrial populations include the Finnish metapopulation of the moth *Amphipyra perflua*. This system has long been known for occasionally experiencing sudden increases in abundance at a regional scale (Mikkola and Jalas 1979). It has been hypothesized that local populations behave sporadically as outbreak foci and provide bursts of immigrants to nearby patches, thereby causing regional flushes (Hanski 1985); yet what causes one or more populations to grow large locally in the region of the outbreak is unknown (Mikkola 1979, Hanski 1985).

Outbreaks in the spruce budworm *Christoneura fumiferana* dynamics have also received considerable attention (for a review see Royama 1992). Budworm outbreaks have been recurrent in the past two centuries. The pattern was not local but observed widely over eastern Canada and the adjacent areas of the United States. Most local populations tended to oscillate more or less in unison. Seven bursts in budworm abundance have been reported since 1710 in Quebec (Royama 1992), separated by time intervals of 25 to 75 years. More accurate data collected in recent years in New Brunswick show that all local populations have reached their peaks more or less simultaneously.

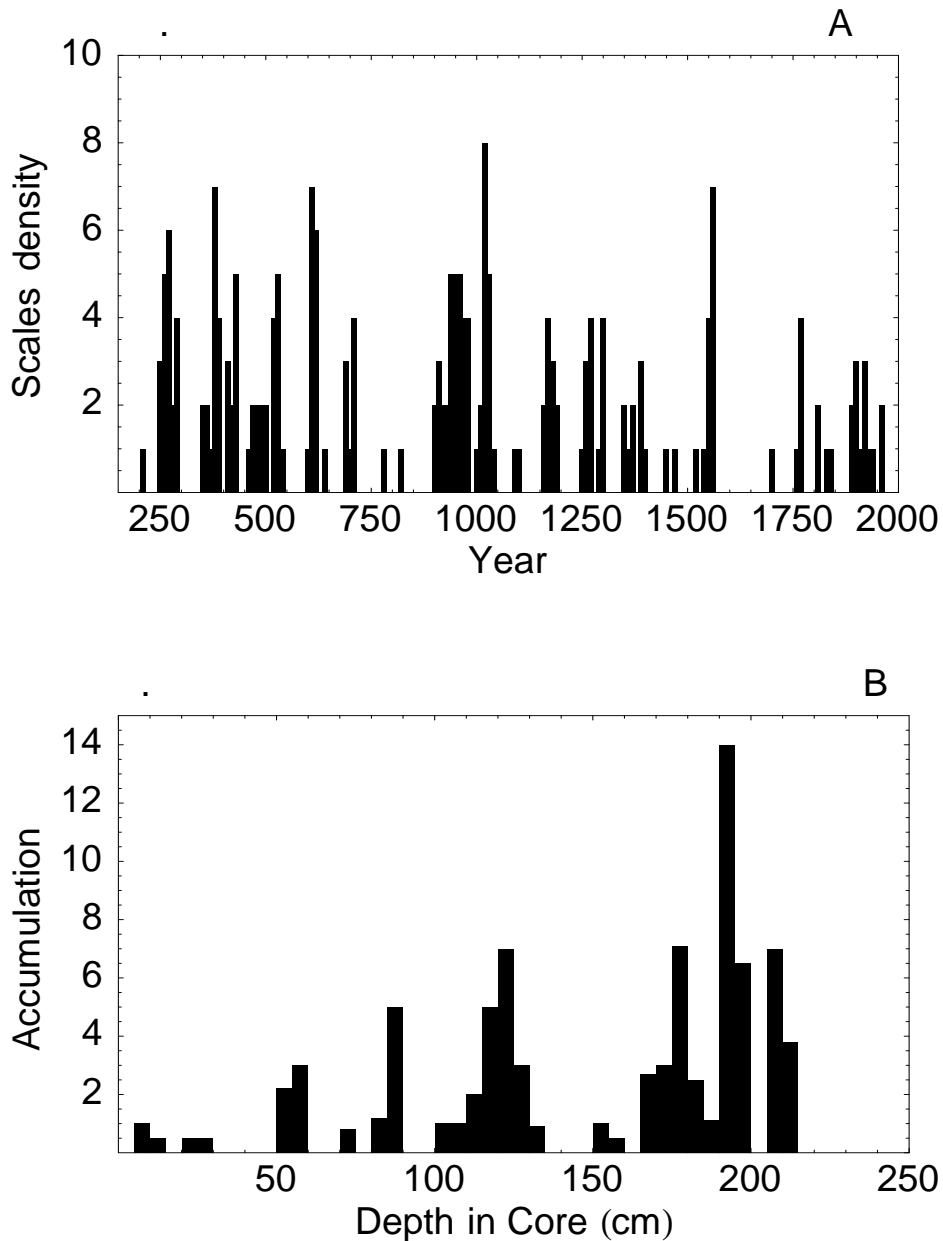


FIG. 1. Intermittent rarity in the Pacific sardine over the past two millennia (A), and during the whole Holocene period (B). In (B), the correspondence between depth in core and timescale is roughly linear piece-wise. The depth interval 0-50cm corresponds to present-500 yr BP; 60-140cm, to 1,800-2,500 yr BP; 150-190cm, to 3,000-3,250 yr BP; 195-220cm, to 11,400-11,700 yr BP. Each datum comes from the density of fish scales and debris in marine petroleum cores. Scales' densities have been shown to correlate very strongly with fish density (Baumgatner et al. 1992). Cores from different basins produce similar fluctuations, peaking and declining simultaneously. Redrawn from Soutar and Isaacs (1974) and Baumgatner et al. (1992) (A) and DeVries and Percy (1982) (B).

Theoretical Background: Invasibility and Coexistence

In the next Section, we formulate a simple mechanism for intermittent rarity in terms of weak invasibility in a fluctuating community. Here we briefly review the underlying theoretical issues. We consider a community comprising k species. Let $X_i(t)$ be the population density of species i at time t . At time $t+1$, the density of species i is given by:

$$(1) \quad X_i(t+1) = f_i[X_1(t), \dots, X_k(t)]X_i(t).$$

The term $f_i[X_1(t), \dots, X_k(t)]$ denotes the instantaneous geometric rate of increase of species i , which is potentially influenced by the densities of all k species. The community dynamics can be described by an internal attractor in a k -dimensional phase space, each axis corresponding to the density of species 1, ..., k . The dynamics of species i when all other species have zero density is characterized by a 'single-species' attractor which lies on the i th axis.

To see if species i persist in the system, one can use the invasibility criterion introduced by Turelli (1978) and elaborated by Chesson and Ellner (1989), Metz et al. (1992), Rand et al. (1994) and Ferriere and Gatto (1995). The invasibility criterion involves the quantities

$$(2) \quad \chi_i = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \chi_i(t)$$

defined for each species. In this equation $\chi_i(t)$ stands for the multiplicative growth rate of species i calculated in the limit as its density tends to 0, that is

$$(3) \quad \chi_i(t) = \ln f_i[\hat{X}_1(t), \dots, \hat{X}_k(t)]$$

with $\hat{X}_i(t) \equiv 0$ and all other $\hat{X}_j(t)$ follow the time-evolution given by Eq. (1) with the density of species i set to zero. We shall refer to $\chi_i(t)$ and χ_i as the 'instantaneous invasion exponent' and the 'long-term invasion exponent' (or simply 'invasion exponent') of species i . The latter measures the long-run growth rate of species- i at

extreme rarity. The invasibility criterion says that the community persists if all species have positive long-term invasion exponents: any of them could eventually rebound should it decline to very low density.

Notice that if densities $\hat{X}_1(t), \dots, \hat{X}_k(t)$ fluctuate through time, so will the instantaneous invasion exponent. Provided that the community model assumes standard ergodic properties (e.g., Tuljapurkar 1990), the mean of the statistical distribution of instantaneous invasion exponents should be equal to the long-term invasion exponent.

There are well-known community models covered by Eq. (1). When density-dependence is of Ricker-type, i.e.

$$(4) \quad f_i[X_1(t), \dots, X_k(t)] = \exp[r_i - a_{i1}X_1(t) - \dots - a_{ik}X_k(t)],$$

we obtain the natural analogue in discrete time of a Lotka-Volterra model (Hofbauer et al. 1987). Competition parameters a_{ij} measures the strength of competition exerted by species j on species i . This model is appropriate to describe the dynamics of a community of interacting semelparous species. Here the instantaneous invasion exponent of, say, species k is

$$(5) \quad \chi_k(t) = r_k - a_{k1}\hat{X}_1(t) - \dots - a_{kk-1}\hat{X}_{k-1}(t),$$

and the long-term invasion exponent is

$$(6) \quad \chi_k = r_k - a_{k1}\langle \hat{X}_1 \rangle - \dots - a_{kk-1}\langle \hat{X}_{k-1} \rangle$$

where $\langle \hat{X}_j \rangle$ denotes the temporal average of species j density in the absence of species k . This time-discrete Lotka-Volterra model can be extended to encompass iteroparous species, using

$$(7) \quad f_i[X_1(t), \dots, X_k(t)] = s_i + \exp[r_i - a_{i1}X_1(t) - \dots - a_{ik}X_k(t)].$$

Parameter s_i is the per capita adult survival rate and the exponential term is the per capita rate of recruitment to the adult population (Warner and Chesson 1985). There

are no simple formula for the instantaneous and long-term invasion exponents. For species k , one has:

$$(8) \quad \chi_k(t) = \ln \left\{ s_k + \exp \left[r_k - a_{k1} \hat{X}_1(t) - \dots - a_{kk-1} \hat{X}_{k-1}(t) \right] \right\}$$

and

$$(9) \quad \chi_k = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln \left\{ s_k + \exp \left[r_k - a_{k1} \hat{X}_1(t) - \dots - a_{kk-1} \hat{X}_{k-1}(t) \right] \right\}.$$

Although such « mean-field » deterministic models have been a mainstay of theoretical ecology, there is increasing recognition that they may fail to capture essential aspects of community dynamics, which result from the discreteness of individuals, the stochastic nature of life histories and the spatial localisation of interactions between individuals (Durrett and Levin 1994, Tilman and Kareiva 1997, Dieckmann et al. in press). However, we emphasize that the Ricker density-dependence offers itself as a remarkable exception, since it can be rigorously derived as a deterministic approximation of a stochastic, spatial individually-based model of competition (Royama 1992, Leitner *submitted manuscript*). Therefore, Eqs. (4) and (5) offer sound models of communities of interacting species, that lend themselves to tractable analysis while retaining the essence of the stochastic spatial processes operating at the individual level.

A Universal Mechanism Causing Intermittent Rarity

Intermittent rarity due to weak invasibility in a fluctuating community

In this section we present a simple mechanism for intermittent rarity. We introduce a prototypical model governing the dynamics of a particular species, called X , within a community. We assume that the X population is affected by both intra and interspecific competition, whereas the other populations are not influenced by species X . We describe the X population dynamics by making use of a Lotka-Volterra type equation (see Eq. (4)):

$$(10) \quad X(t+1) = \exp[r - a_1 X(t) - a_2 Y(t)] \cdot X(t)$$

where $X(t)$ is the density of species X at time t and $Y(t)$ denotes a combination of densities of the other species in the community, which we call the 'background community'; a_1 and a_2 are competition coefficients. In this section, the Y dynamics are treated as a 'black box' that does not need explicit modelling. If the background community settles on a stable equilibrium Y^* , according to Eqs. (5) and (6) we have

$$(11) \quad \chi = \chi(t) = r - a_2 Y^* \quad \text{for all } t$$

(compared to Eqs. (5) and (6), no hat is needed on Y because we are assuming that the background community is not affected by competition with species X). The coexistence criterion based on invasibility (see previous Section) says that species X persists if r is larger than $a_2 Y^*$. As r assumes lower values that get close to $a_2 Y^*$, species X invasion exponent decreases and the population must settle on a stable equilibrium given by

$$(12) \quad X^* = \chi / a_1.$$

Thus, as species X becomes a weaker invader, its population equilibrium density tends to be very low: species X displays a state of permanent rarity.

A new phenomenon arises when the background community density fluctuates through time. Now the instantaneous and long-term invasion exponents of species X are

$$(13) \quad \chi(t) = r - a_2 Y(t)$$

and

$$(14) \quad \chi = r - a_2 \langle Y \rangle$$

(cf Eqs. (5) and (6)). The new feature is that if r is very close to $a_2 \langle Y \rangle$, which implies that species X is again a weak invader, the statistical distribution of instantaneous invasion exponents is likely to span both positive and negative values around its

mean χ (which is positive but very small). The X population may thus experience negative growth over arbitrarily long periods of time, for the population growth rate in any finite period of time is equal to the arithmetic mean of instantaneous invasion exponents experienced during that period. As a result, phases of extreme rarity develop. Likewise, occasional higher frequencies of positive instantaneous invasion exponents allow population recovery and the return to phases of high density. Intermittent rarity is typified by this alternation of rarity phases of highly irregular durations, and phases of commonness.

An example is shown in Fig. 2, where the background community process $Y(t)$ is modelled as a sequence of independent normally distributed random variables. In general, such temporal fluctuations in the background community may be thought of as deviations from an equilibrium or cyclic density due to environmental stochasticity, or as deterministic chaos. The figure shows intermittent rarity developing as the invasion exponent decreases while the background community dynamics remain driven by the same process (Figs 2A-C). On a logarithmic scale (Figs 2D-F), one can see that the X population can reach very low densities during rarity phases, with a decreasing minimum as the invasion exponent decreases. Also, logarithmic plotting makes it apparent that density fluctuations over rarity phases resemble those observed at higher levels of abundance. As explained above, intermittent rarity results from the statistical distribution of instantaneous invasion exponents spanning negative and positive values almost evenly (Figs 2G-I).

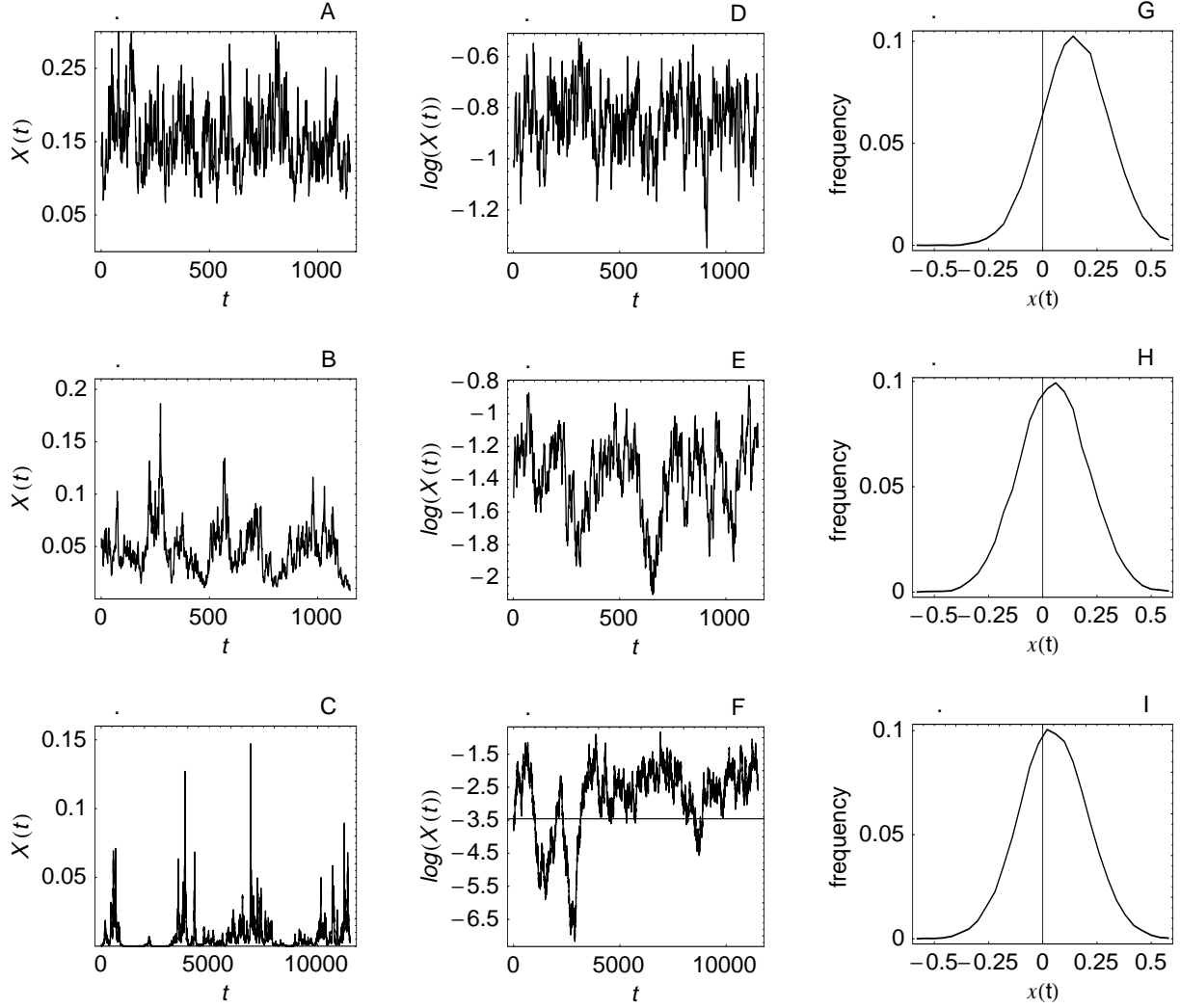


FIG. 2. Dynamics of a population driven by the prototypical model Eq. (10). The background community process is an equilibrium with superimposed white noise (equilibrium value $a_2 Y^* = 1.5$, Gaussian noise with zero mean and variance equal to 0.25). Panels (A)-(C) show the temporal dynamics of species X as its invasion exponent is reduced. Without loss of generality, competition coefficient a_1 is rescaled to 1. In (A), $r = 1.65$ hence $\chi = 0.15$, in (B) $r = 1.55$ hence $\chi = 0.05$, in (C) $r = 1.51$ hence $\chi = 0.01$. Intermittent rarity is visible in panel (C). Panels (D)-(F): same as (A)-(C) but densities are shown on a logarithmic scale. The minimum density approaches zero as the invasion exponent decreases. In (F) the horizontal line indicates the rarity threshold (0.1% of maximum density). Logarithmic plot (F) demonstrates that ups and downs exhibited by the time series below the rarity threshold are similar to fluctuations displayed at higher density levels. Panels (G)-(I): Statistical distributions of instantaneous invasion exponents. The mean equals χ , and as χ decreases, the distribution support spans a larger range of negative values. This begets intermittent rarity.

Recently, intermittent dynamics have been observed in the study of a one-dimensional deterministic model of frequency-dependent selection (Gavrilets and Hastings 1995). One may thus ask whether the mechanism inducing this kind of intermittency (a global bifurcation, or « crisis ») as well as other classical mechanisms for intermittency known in physics (Pomeau and Manneville 1980; see Schuster 1989 for a review) might also be operating in the simplest one-species Ricker model $X(t+1) = \exp[r - X(t)] \cdot X(t)$ and might perhaps suffice to explain the occurrence of intermittent rarity. The intuitive idea is that with no more than overcompensating density-dependence, the species will go directly from peak density to a very low density. There is then essentially exponential growth out of that trough. The length of time in the rare phase depends simply on how deep the initial trough is and how fast population growth is at low density. More precisely, if rarity is defined as density being lower than a threshold ε , then the maximum duration of a rarity phase is easily found to be $T_{\max} = (\ln \varepsilon - \ln X_{\min})/r$ with $X_{\min} = e^{r - X_{\max}} X_{\max} = \exp(2r - 1 - e^{r-1})$; hence $T_{\max} = (\ln \varepsilon + e^{r-1} - r)/r$. One may think of long-lasting rarity phases as being caused by very low minimum population size X_{\min} , or equivalently very large maximum population size X_{\max} . Larger values of X_{\max} are obtained by increasing r . Yet with r equal to 4 for example, we find that rarity phases could not exceed $T_{\max} = 3$ only (setting conservatively $\varepsilon = 1$); with $r = 6$, T_{\max} is less than 24 time units. This means that intermittent rarity does not develop here. The reason is that increasing r may lower the minimum population density but it concomitantly accelerates the rate at which the population leaves the range of low abundance. Alternatively, rarity might be caused by extremely slow growth from low density, i.e. r being only slightly greater than 1. But then $T_{\max} \approx \ln \varepsilon / r$ which again may not be large. Thus classical mechanisms for intermittency reviewed by Schuster (1989) cannot generate intermittent rarity in our prototypical model (also see Rogers 1984). The argument extends to generic one-dimensional models $X(t+1) = f[X(t)] \cdot X(t)$ where $f[X(t)]$

denotes the instantaneous population growth rate; only in the degenerate case $X_{\min} = f(X_{\max})X_{\max} = 0$ may intermittent rarity develop if $f(0)$ is very close to 1.

Universality in the distribution of rarity times

An important characteristic of intermittent rarity dynamics is the sequence of times elapsed between successive outbreak events, or rarity times. The statistical distribution of rarity times has practical importance, as it provides a way of estimating the likelihood, at any time, of entering a rarity episode of a given duration. The distribution of rarity times is easily measured: given a rarity threshold ε , a rarity episode of length T for species X is defined by

$$(15) \quad X(0) > \varepsilon, X(1) \leq \varepsilon, X(2) \leq \varepsilon, \dots, X(T) \leq \varepsilon, X(T+1) > \varepsilon$$

(for a suitably shifted time origin). Figure 3 displays a double logarithmic plot of the distribution of rarity episodes corresponding to the time series $X(t)$ shown in Fig. 2C. The pronounced linearity of the graph expresses the fact that the likelihood $P(T)$ of rarity episodes of duration T decays as a power law in that duration. The fitting form is

$$(16) \quad P(T) \propto T^\gamma$$

with $\gamma \approx -3/2$. The distribution does not depend upon the rarity threshold ε , as long as ε be small enough to stand within the linear domain of the map Eq. (10) (near to $X = 0$). The power law implies that there are rarity phases of arbitrary length. Thus, the question “how long is a typical rarity phase?” has no answer: species X exhibits intermittent rarity on all timescales. Also, the temporal patterns of ups and downs are similar at all density levels (see Figs 2D-F), a fact which underlies the fractal properties of intermittently rare time series. These fractal properties can actually be used to derive a formal proof of the existence of the $-3/2$ power law (see Venkataramani et al. 1995, 1996; and Appendix 1).

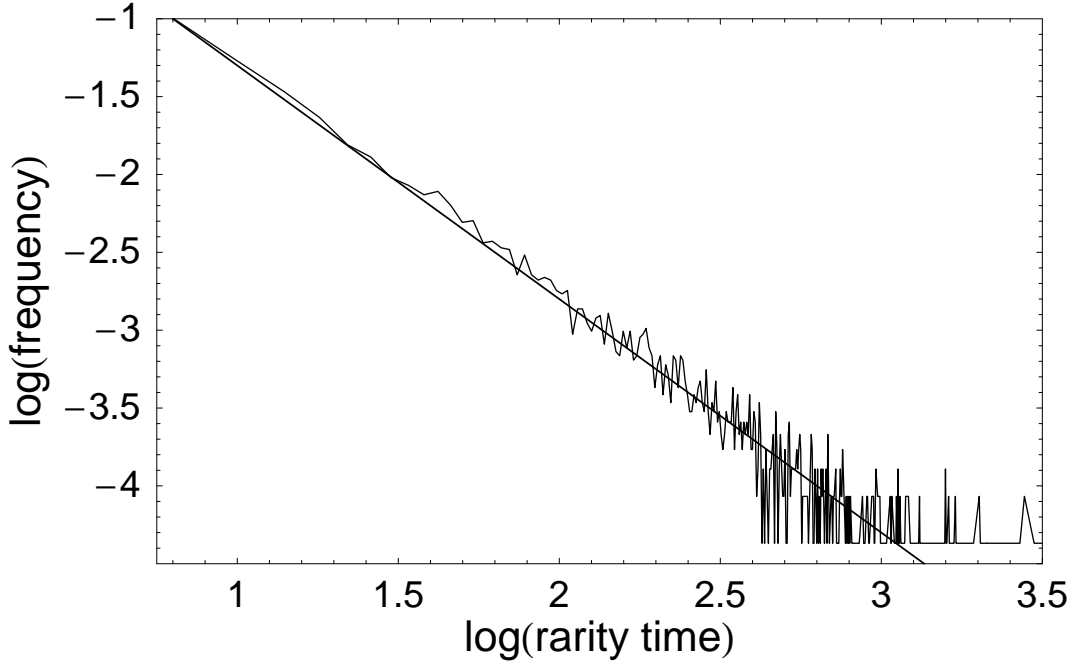


FIG. 3. Power-law distribution of rarity times for a population driven by the prototypical model Eq. (10) (rescaled with $a_1 = 1$). On this log-log plot, the distribution $P(T) \propto T^{-\gamma}$ is well fitted by a straight line with slope $-3/2$ (as shown). The corresponding time series $X(t)$ is displayed in Fig. 2C. A total of 2,000,000 iterations of Eq. (10) were used to construct this distribution.

Scale-free dynamics and power laws are known in physical sciences to characterize systems formed of many interacting subunits which are poised at a ‘critical point’, where two or more macroscopic phases become indistinguishable (Stanley 1971). The property of scaling goes along with the concept of ‘universality’ which entails that quite different systems can behave in a very similar fashion near their respective critical states. Thus, at a critical point, many of the precise details of the interactions between constituents of the system play virtually no role whatsoever in determining the scaling property of the system (Baxter 1982, Stanley 1995). We now probe the universality of the scaling property of intermittent rarity by analysing the dynamics of several two-species discrete-time competition models.

Intermittent Rarity in a Two-Species Model

The above description of a simple mechanism underlying intermittent rarity is based on the fundamental assumption that there is no feedback of the intermittently rare

species on the background community. We now examine the consequences of relaxing this assumption. To this end, we consider a two-species version of the general community model introduced by Warner and Chesson (1985) and involving Ricker-like density-dependence (Eq. (7)). Our study continues from Gatto's (1993) preliminary investigation of coexistence in such a model. Whereas the basic Ricker model was intended to model Pacific salmon populations and assumed discrete generations, Gatto (1993) addressed the case where a small fraction of adults of two species survive after reproduction, and within and between-species competition effects are the same on the recruitment of both species. Gatto's model reads

$$(17.1) \quad X_1(t+1) = s_1 X_1(t) + \exp[r_1 - a_1 X_1(t) - a_2 X_2(t)] X_1(t)$$

$$(17.2) \quad X_2(t+1) = s_2 X_2(t) + \exp[r_2 - a_1 X_1(t) - a_2 X_2(t)] X_2(t)$$

which can be rescaled such that $a_1 = a_2 = 1$. Coexistence may occur through the so-called « storage effect » (Warner and Chesson 1985) provided that single-species dynamics do not correspond both to stable equilibria. The community attractor may then be a stable equilibrium, a cycle, a quasicycle or a strange attractor (Gatto 1993).

A detailed mathematical analysis of Eqs. (17) is beyond the scope of this paper. Instead, we concentrate on selected examples chosen to investigate how the model conforms to the general predictions obtained in the previous Section.

We first consider the model Eqs. (17) with species 1 parameters set to $s_1 = 10^{-2.3}$ and $r_1 = 3.7$. These values, that might be representative of a nearly semelparous marine fish species as envisaged by Gatto (1993), generate chaotic population dynamics. The storage effect can operate and there exists a range of species 2 parameters that allow for coexistence with species 1. This coexistence region is shown on Fig. 4A. It encompasses all species 2 parameter values for which mutual invasibility occurs, that is, $\chi_1 > 0$ and $\chi_2 > 0$. Inside the coexistence region, the long-term invasion exponent of species 2 decreases smoothly towards zero as one approaches the invasion boundary $\chi_2 = 0$. Thus, near to this boundary, all trait

values correspond to ‘weakly invading’ species which are characterized by a very low long-term invasion exponent.

To examine whether there exist regions in the parameter space that are conducive to intermittent rarity in species 2, we define a rarity index (between 0 and 1) as the length of the longest episode spent by $X_2(t)$ below a rarity threshold, relative to the total duration of a simulation run. Large values of the rarity index indicate that intermittent rarity may develop. Figure 4B plots the rarity index across species 2 parameter space while species 1 parameters are fixed as above. A high rarity index is observed all along the invasion boundary $\chi_2 = 0$ (see Fig. 4A). Varying species 2 parameters such that χ_2 increases from zero results in a decreasing rarity index.

Then we examine the dynamics of the system when species 2 is a weak invader with a high rarity index. The shape of a typical community attractor and trajectories are shown in Fig. 5. The community attractor is chaotic with a very skewed shape (Fig. 5A), showing a marked accumulation of points near to the species 1 axis. Thus, species 2 spends much time at very low density. Whereas no particular pattern emerges from the chaotic dynamics of species 1 (Fig. 5B), the behavior of species 2 does exhibit the two qualitatively distinct, intermittent states which are typical of intermittent rarity (Fig. 5C): the state of rarity which seems nearly constant, close to zero density, and can remain so for very long periods of time; and the bursting state, departing quickly from, and returning quickly to, the rarity state. This dynamical pattern is not transitory and persists on the long run.

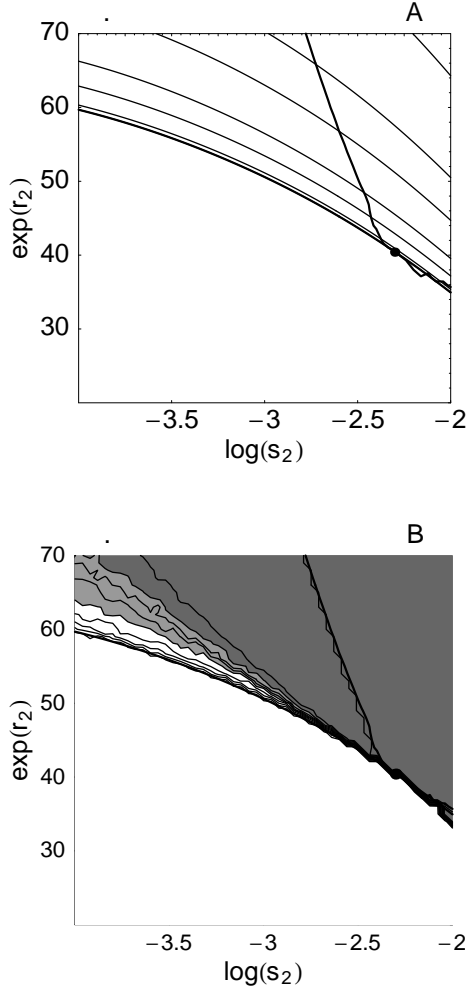


FIG. 4. (A) Coexistence diagram for the two-species Gatto model Eqs. (17). Without loss of generality, competition coefficients a_1 and a_2 are rescaled to 1. Life-history parameters of species 1 are fixed to $s_1 = 10^{-2.3}$ and $r_1 = 3.7$ (black circle). Bold lines correspond to zero invasion coefficients χ_1 and χ_2 . Life-history traits s_2 and r_2 permitting coexistence with species 1 are comprised between these two lines. Thin lines are contour lines for χ_2 at the following levels: 0.01, 0.05, 0.1, 0.2, 0.3, 0.5. (B) Rarity diagram. The diagram shows contours of a rarity index (between 0 and 1; see text for details) for species 2 in the Ricker-Gatto model, Eqs. (17). Dark grey: 0–0.2; light grey: 0.2–0.5; white: >0.5. Intermittent rarity develops across the white area overlapping the coexistence region. Parameter values for species 1 (black circle) are the same as in panel (A). *Numerical methods:* (A) We calculated invasion exponents from Eq. (9). The time series $\hat{X}_i(t)$ were computed after discarding 5,000 time steps corresponding to transient behavior. Then the sum in Eq. (9) was taken over the 5,000 next time steps. Species 2 parameters were sampled over a 100×100 grid. Initial conditions: $X_1(0) = 10.0$, $X_2(0) = 10.0$. (B) The rarity index was computed over 50,000 time steps, after eliminating 5,000 transitory iterates. The rarity threshold was set to 1% of the maximum density reached by species 2 over 50,000 iterates.

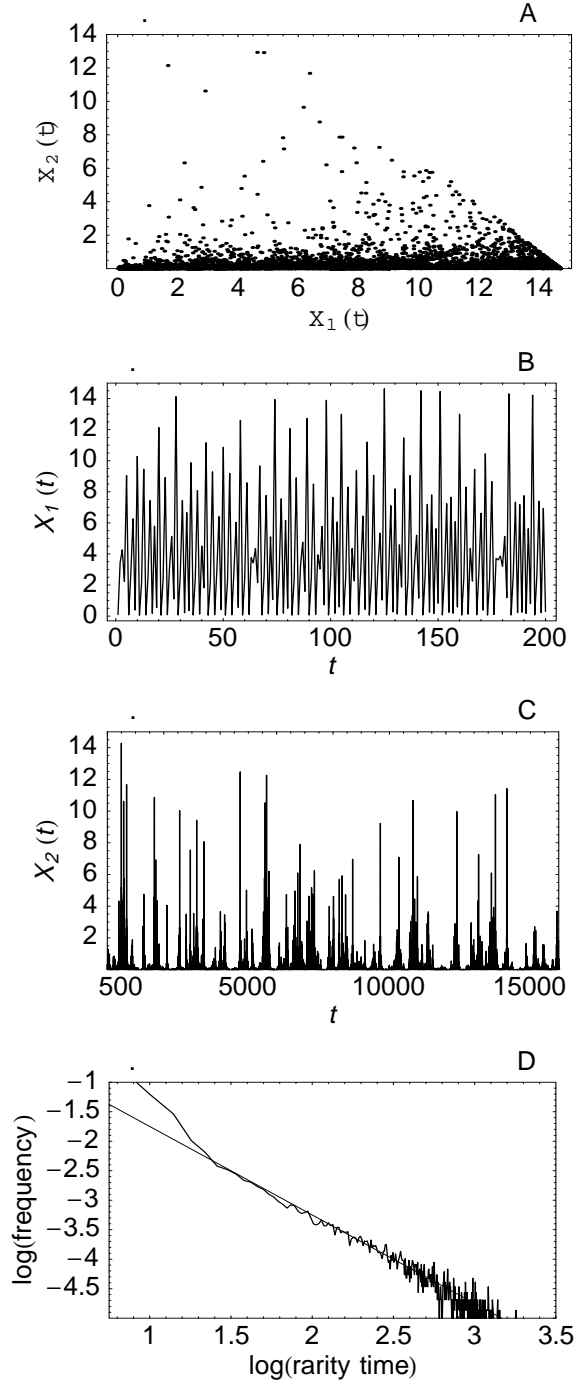


FIG. 5. Exemplary dynamics for the Gatto model Eqs. (17) when species 2 is a weak invader ($\chi_2 = 0.017$). Parameter values for species 1 are the same as in Fig. 4. Parameter values for species 2 are: $s_2 = 10^{-3.52}$, $r_2 = 4.04$. (A) Community attractor. (B) Plot of species 1 density vs. time. Dynamics are chaotic, with no apparent pattern. (C) Plot of species 2 density vs. time. Species 2 is intermittently rare. (D) Power-law distribution of rarity times. The thin straight line has slope $-3/2$. The rarity threshold was set to 1% of maximum species 2 density.

The reason why the weak invasibility condition for intermittent rarity found in the prototypical model extends to the Gatto two-species model can be understood from the mathematical analysis of De Feo and Ferriere (*submitted manuscript*; also see Haderler and Gerstmann [1990] and Neubert and Kot [1992]). In the community phase space, a positive invasion exponent for species 2 means that the single-species 1 attractor is ‘transversally’ unstable: a small perturbation in the direction of the species 2 axis results in a trajectory that diverges from the species 1 axis into the interior of the phase space. When the single-species 1 attractor is chaotic, it contains infinitely many unstable cycles (e.g., Ruelle 1989). Mathematically, one can still define the invasion exponent of species 2 with respect to any of these cycles: Eq. (3) still applies, with $X_1(t)$ taking values on the cycle. The transverse instability of the whole chaotic attractor can then be interpreted in terms of the transverse stability and instability of each of the cycles ‘hidden’ in the chaotic attractor. A slightly positive invasion exponent means that there are slightly more cycles that are transversally unstable. Transversally unstable periodic orbits will repel the community trajectory away from the species 1 axis, whereas the transverse stability of the other cycles will attract it back close to the axis. The resulting burst-and-crash dynamics is akin to what mathematicians call a ‘heteroclinic cycle’ (e.g., Hofbauer 1994, Krupa 1997) which forms the backbone of the chaotic community attractor observed in simulations like those reported in Fig. 5A (Mira 1987, Dellnitz et al. 1995).

Figure 5D shows that the statistical distribution of rarity times generated by the Gatto model in the dynamics of species 2 is identical to the $-3/2$ power law found in the prototypical model Eq. (10). This happens in spite of the correlation structure present in the chaotic dynamics of the competing species 1, whereas in the prototypical model the background community dynamics $Y(t)$ assumed no temporal autocorrelation. In fact, the chaotic dynamics $X_1(t)$ have a characteristic timescale beyond which their autocorrelation is negligible. If the invasion exponent of the intermittently rare species is small enough, the typical time between bursts is likely

to be much longer than the autocorrelation time of $X_1(t)$, which leaves the power law found in the prototypical model basically unchanged. Only the observed frequency of very short rarity episodes extends above the fitted power law. Short-term negative autocorrelations in the chaotic species 1 dynamics are likely to be responsible for this slight over-representation of short rarity phases, by increasing the chance that a negative instantaneous invasion exponent be followed by a positive one.

Robustness of the $-3/2$ Power Law

Here we probe further the robustness of the $-3/2$ power law. First, one can vary the species' demographic parameters considerably in Eqs. (17) without affecting the conditions for, and statistical properties of, intermittent rarity in species 2. We were able to classify all coexistence and rarity diagrams that we have studied numerically into three categories according to their qualitative geometrical features. One category is typified by the example studied above (Figs 4 and 5). Figure 6 displays exemplary intermittent time series that pertain to the two others. Although the dynamics across bursting episodes look qualitatively very different (insets in Figs 6A and 6B), rarity phases possess the same statistical property: they are distributed according to a power law with exponent very close to $-3/2$ (Figs 6A and 6B).

Second, we examine the effect of including environmental stochasticity in the model. In general, we know that weak invaders in the deterministic case remain so in the stochastic setting if noise amplitude is small, for long-term invasion exponents are stable to small perturbations (Ferriere and Gatto 1995). We have incorporated environmental noise in the Gatto model as multiplicative, uncorrelated perturbations (e.g., Dennis et al. 1995). Equations (17) are replaced by

$$(18.1) \quad X_1(t+1) = \{s_1 X_1(t) + \exp[r_1 - a_1 X_1(t) - a_2 X_2(t)] X_1(t)\} \exp[W_1(t)]$$

$$(18.2) \quad X_2(t+1) = \{s_2 X_2(t) + \exp[r_2 - a_1 X_1(t) - a_2 X_2(t)] X_2(t)\} \exp[W_2(t)] .$$

where $W_1(t)$ and $W_2(t)$ are independent, Gaussian random variables with zero mean and time-independent variances. Figure 6C shows the distributions of rarity phases for three levels of environmental noise. Species 2 is still a weak invader at all noise levels, and the distributions remain accurately fitted by a power law with exponent $-3/2$.

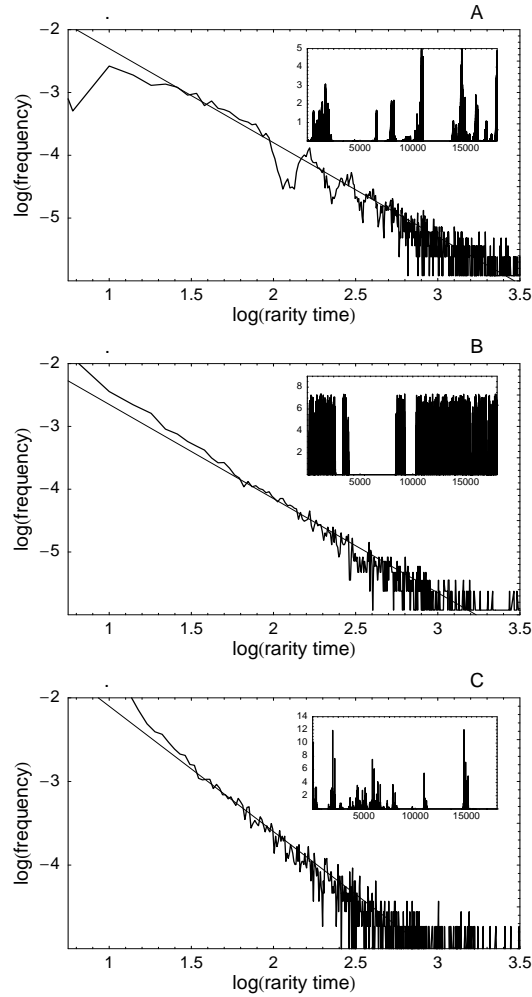


FIG. 6. Robustness of the power-law distribution of rarity times in the Gatto model Eqs. (17). (A) and (B) display the power law for other combinations of parameters in Eqs. (17), which typify the possible geometries for the community attractor in this model. In (A) $s_1 = 10^{-2.3985}$, $r_1 = 3.4$, $s_2 = 10^{-1.7}$, $r_2 = 2.815$. In (B) $s_1 = 10^{-3.934}$, $r_1 = 3.8795$, $s_2 = 10^{-2}$, $r_2 = 3.1$. In (C) parameters are the same as in Fig. 5 but environmental noise is added according to Eqs. (18) with noise variance equal to 10^{-3} ; the distribution was computed for a population trajectory that did not go extinct over 2,000,000 iterations. In all cases, species 2 is a weak invader ($\chi_2 = 0.006$ in [A], $\chi_2 = 0.009$ in [B] and [C]) and intermittent rarity develops (insets). All thin lines' slope is $-3/2$.

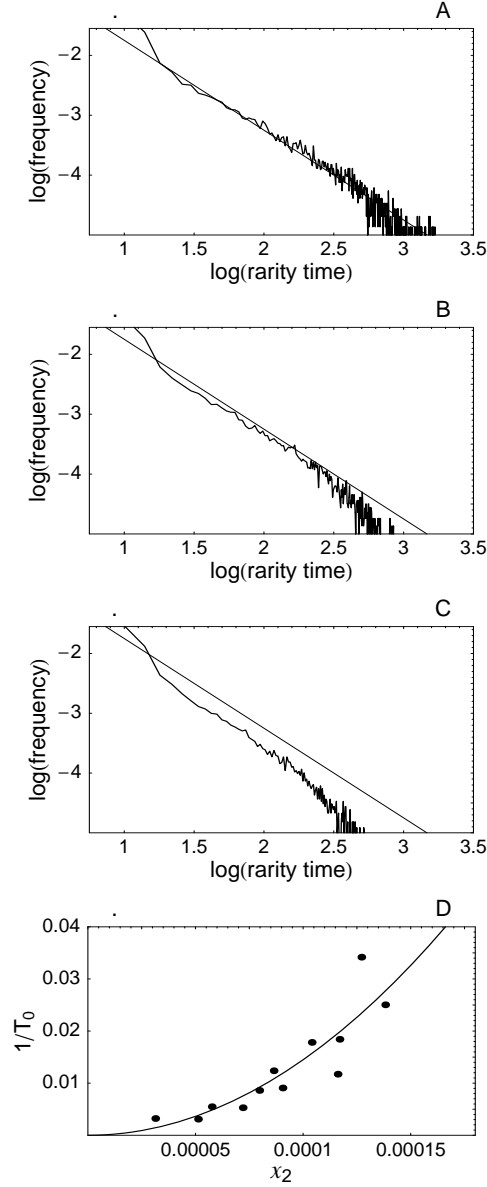


FIG. 7. Influence of species 2 invasion exponent χ_2 on the distribution of rarity times. Species 1 parameters are the same in all panels (values as in Figs. 4). (A) to (C): Log-log plot of the distribution of rarity times for different invasion exponents obtained by varying s_2 : $s_2 = 10^{-3.52}$ and $\chi_2 = 0.017$ in (A) (same as in Fig. 5), $s_2 = 10^{-3.42}$ and $\chi_2 = 0.032$ in (B), $s_2 = 10^{-3.32}$ and $\chi_2 = 0.046$ in (C). Parameter r_2 is fixed ($r_2 = 4.04$). (D) Inverse average rarity time plotted against the invasion exponent. Values of parameters r_2 and s_2 were randomly sampled within ranges 3.95–4.05 and $10^{-3.55} - 10^{-3.50}$, respectively. The set of points is well fitted by a quadratic curve: $1/T_0 = 1.4485 \cdot 10^6 \chi_2^2$. Note that as the rare species becomes a weaker invader (χ_2 tends to zero), $1/T_0$ tends to zero, implying that the average rarity time becomes arbitrarily large, and the distribution of rarity times approaches a power law.

Finally, the theory of critical phenomena predicts that as one smoothly moves the system away from the critical state, power laws should bend down with an exponential falloff (see, e.g., Csilling et al. 1994). This actually happens in the Gatto model, as shown in Fig. 7. As the long-term invasion exponent χ_2 increases from very low values, the distribution of rarity phases changes to better fit the form

$$(19) \quad P(T) \propto T^\gamma \exp(-T/T_0)$$

where T_0 is the characteristic average rarity phase (Figs. 7A-C). In general, we find that the inverse characteristic time $1/T_0$ increases from zero with the long-term invasion exponent χ_2 according to a quadratic relation

$$(20) \quad 1/T_0 \propto \chi_2^2,$$

(Fig. 7D), although the coefficient of proportionality seems dependent upon species 1 parameters.

The effect of demographic stochasticity

During periods of rarity, the species will be at risk of extinction due to demographic stochasticity. We now examine how this affects the power-law distribution of rarity times. The prototypical model and the Gatto model describe the population dynamics in terms of a continuous dynamical variable. This is a valid approximation in the limiting and idealized case of an infinite ‘system size’. Here the system size, denoted by K , depends on the individual’s requirements and environmental resources—a notion which corresponds in individually-based models to that of a carrying capacity (Royama 1992, Leitner *submitted manuscript*). We derive a stochastic description of the Gatto model, in which the finite system size and integer structure of the population is taken into account (see e.g. Nisbet and Gurney 1982).

Species density X is merely defined as population size N (an integer number) divided by K . We assume that each individual’s survival probability follows a binomial distribution with mean s_i ($i = 1, 2$). Individual recruitment at time t is

drawn at random from a Poisson distribution with mean $\exp[r_i - N_1(t)/K - N_2(t)/K]$ ($i = 1, 2$). The Gatto model then becomes

$$(21.1) \quad N_1(t+1) = \sum_{n=1}^{N_1(t)} \text{Binom}(s_1) + \sum_{n=1}^{N_1(t)} \text{Poisson} \left(\exp \left[r_1 - a_1 \frac{N_1(t)}{K} - a_2 \frac{N_2(t)}{K} \right] \right)$$

$$(21.2) \quad N_2(t+1) = \sum_{n=1}^{N_2(t)} \text{Binom}(s_2) + \sum_{n=1}^{N_2(t)} \text{Poisson} \left(\exp \left[r_2 - a_1 \frac{N_1(t)}{K} - a_2 \frac{N_2(t)}{K} \right] \right)$$

We have run extensive simulations of this model taking $a_1 = a_2$, and typical outcomes for the distributions of rarity times are reported in Fig. 8. Here the rarity threshold is defined as a percentage of the system size. Our simulations show that the likelihood of extinction during a rarity phase increases as the system size decreases. Extinction due to demographic noise tends to terminate the species lifetime during potentially long rarity phases. As a consequence, we observe the appearance of an exponential falloff in the distribution of rarity phases, which means that long rarity phases become less likely (Fig. 8A). The $-3/2$ power law is recovered from the stochastic Gatto model Eqs. (21) as the system size K increases. For finite values of K , the distribution fits the form given by Eq. (19) which includes an exponential correction. Remarkably, we found yet another algebraic scaling, involving the characteristic average rarity phase T_0 as a function of the system size K . This power-law scaling, shown in Fig. 8B, appears to be robust and parameter-independent. We believe that the theory of perturbed random walks should allow one to elaborate on the proof sketched in Appendix 1 to unravel the mathematical underpinning of this seemingly general relationship.

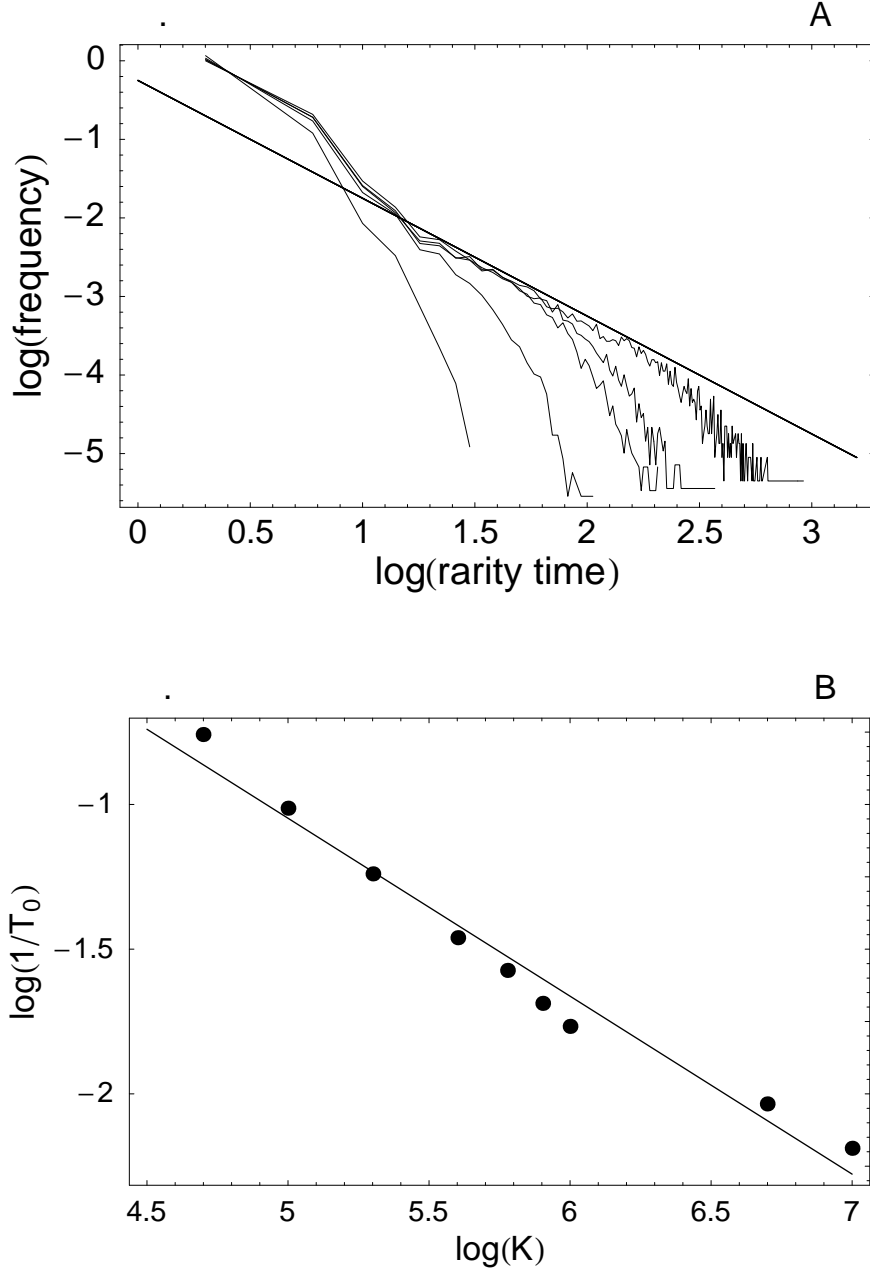


FIG. 8. Effect of demographic stochasticity on the distribution of rarity times. Rarity threshold set to 5% of system size K (carrying capacity). (A) Distributions of rarity times for $K = 5 \cdot 10^4$, $2 \cdot 10^5$, $6 \cdot 10^5$, 10^6 and 10^7 (left to right). For each K , the distribution was computed from the rarity phases produced by a large number of community trajectories governed by the stochastic model Eqs. (21). Rarity phases during which extinction occurs were discarded. As K increases, the distribution approaches a power law with exponent $-3/2$ (indicated by the straight line). For finite K , the average rarity time T_0 is finite and the distribution fit Eq. (19) which involves a negative exponential correction to the power law. (B) Algebraic scaling of the inverse of mean rarity time T_0 with system size K .

Intermittent Rarity in Other Competition Models

We further investigate how robust our findings are by considering two very different versions of Warner-Chesson's community model. First, we assume that two competing species differ in the way individuals cope with crowding. In species 1, intra and interspecific competition adversely affect all individuals equally (scramble competition). In species 2, individuals have an uneven access to the resources and some of them eventually do better than others when the habitat becomes highly populated (contest competition). Franke and Yakubu (1991) used the Hassel-Comins-May and Ricker population growth models to investigate the conditions for exclusion and coexistence in such a system when both species reproduce semelparously. Their model reads

$$(22.1) \quad X_1(t+1) = \exp\{r_1 - c_1[X_1(t) + X_2(t)]\}X_1(t)$$

$$(22.2) \quad X_2(t+1) = \frac{\exp(r_2)}{1 + c_2[X_1(t) + X_2(t)]} X_2(t) .$$

Due to the contest competition mechanism, species 2 possesses a single nontrivial equilibrium density which is always stable. The density of species 1, however, obeys to the overcompensatory Ricker mechanism that produces oscillations and chaos. Alike the Gatto model, the Franke-Yakubu equations assume that both species have equal competitive abilities.

The second model we consider in this section incorporates the effect of « refuges » on the dynamics of host-parasitoid associations. The model is adapted from Hochberg and Hawkins (1993) to the simple case of one parasitoid and two competing hosts. The parasitoid is assumed to be a generalist species whose density is maintained at a constant level by other host species in addition to the two host species considered here. Hosts experience complete invulnerability to parasitoid attack in specific structural refuges. Within refuges, resources are sufficiently abundant to ignore the effects of intraspecific competition. Generations are discrete

and non-overlapping, and during each generation, a proportion of the larval host community is vulnerable to parasitism. The model is given by

$$(23.1) \quad X_1(t+1) = f_1 X_1(t) \left\{ \alpha_1 + (1 - \alpha_1) d[X_1(t), X_2(t)] g[X_1(t), X_2(t)] \right\}$$

$$(23.2) \quad X_2(t+1) = f_2 X_2(t) \left\{ \alpha_2 + (1 - \alpha_2) d[X_1(t), X_2(t)] g[X_1(t), X_2(t)] \right\}$$

where f denotes the average number of offspring produced per host; α is the proportion of the host population that is invulnerable to parasitism; d is the proportion of hosts surviving from intra and interspecific competition outside refuges; and g is the functional response of parasitoids. The competition term involves the Maynard-Smith density-dependence type (Maynard Smith 1974). Both d and g are fully expounded in Appendix 2.

The structure of coexistence and rarity diagrams computed for the Franke-Yakubu and Hochberg-Hawkins models (not shown) lead to the same conclusions as those previously stated for the Gatto model. Intermittent rarity arises in correspondence with weak invasibility and fluctuations in the competing population. In spite of the purportedly disparate structure of these models, power laws with exponent close to $-3/2$ still characterize the dynamics of intermittent rarity (Figs 9A and 9B). For both models, the same power law is observed for all combinations of demographic parameters that generate intermittent rarity; the power law is also stable to white noise (results not shown).

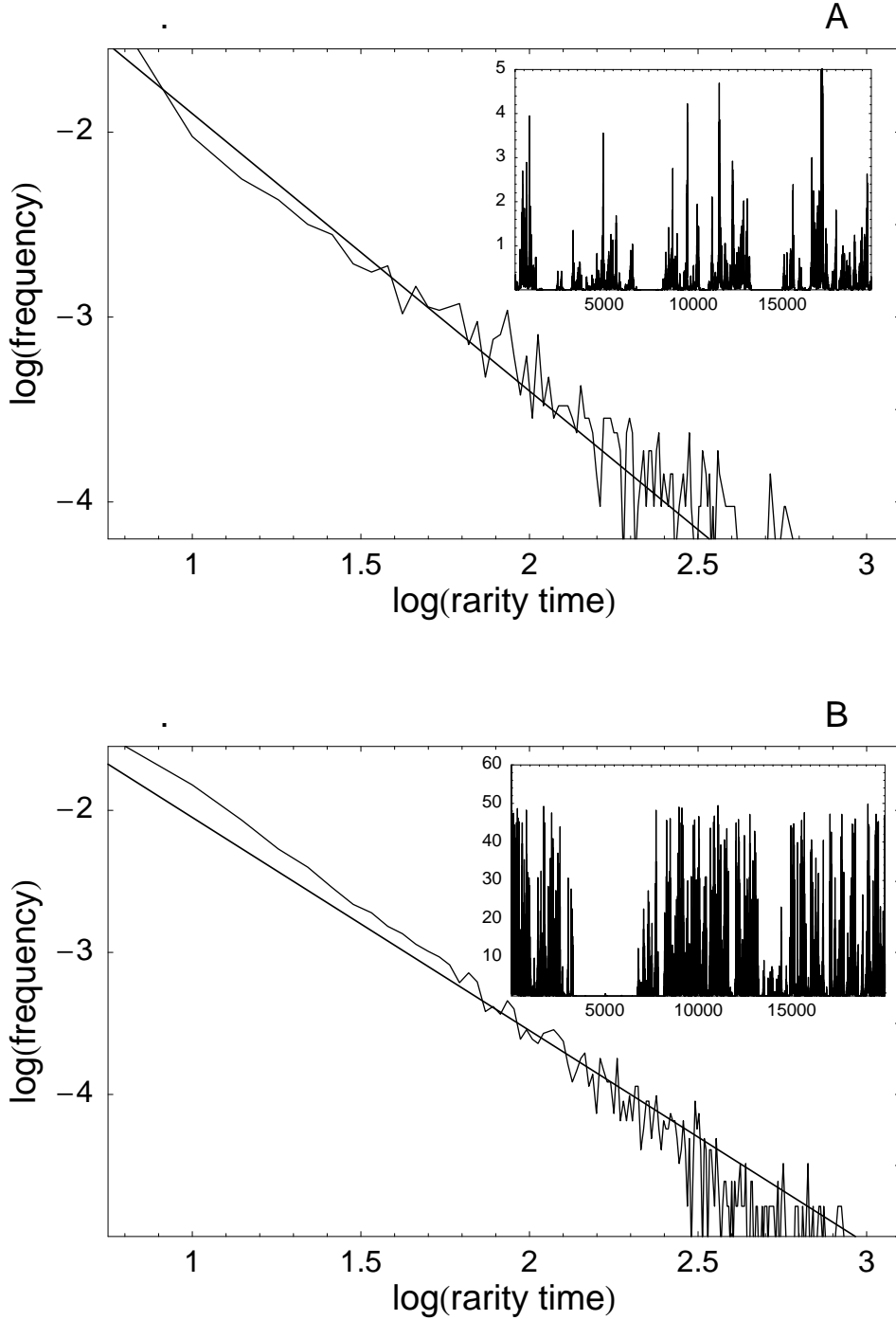


FIG. 9. Power-law distributions of rarity phases and dynamics of intermittent rarity (insets) from two other competition models. (A) Franke-Yakubu model Eqs. (22). Species 1 parameters are $r_1 = 2.916$ and $c_1 = 0.1$ (single-species 1 dynamics are chaotic) and species 2 parameters are $r_2 = 3.0$ and $c_2 = 1.2$. Species 2 invasion exponent: $\chi_2 = 0.022$ (weak invasion). (B) Hochberg-Hawkins model Eqs. (22). Species 1 parameters are $\alpha_1 = 10^{-5}$ and $f_1 = 15.0$ (single-species 1 dynamics are chaotic) and species 2 parameters are $\alpha_2 = 0.018$ and $f_2 = 5.0$. Species 2 invasion exponent: $\chi_2 = 0.00001$ (weak invasion).

Detecting the $-3/2$ Power Law in Real Data

The power laws shown in the previous Sections are based on simulations involving several millions of iterations. One thus should ask how well these power laws are still visible from shorter time series. One way of dealing with smaller sample sizes for the rarity times is not to plot the frequency distribution, but the so-called survival function of rarity times, that is the function $s(t) = P(T > t)$ which gives the frequency of rarity times T larger than t . Given that the probability distribution $P(T)$ is a power law scaling as $T^{-3/2}$, the survival function must also scale algebraically, like $t^{-1/2}$. For a graphical analysis, survival functions are considerably superior to frequency distributions, especially when sample sizes are small.

Figure 10 displays plots of the survival function of intermittent rarity dynamics generated by the Gatto model. The data were obtained by running the model for only 1,500 iterations, and the procedure was repeated several times. The resulting bundle of survival functions turns out to be very consistent with the underlying ideal $t^{-1/2}$ scaling. On the same graph, we have plotted the survival function calculated for the Pacific sardines data shown in Fig. 1A. In spite of the data scarciness, the fit is remarkable. The slight over-representation of short rarity phases predicted by all models we have considered is even perceivable. This, we believe, brings strong support to the hypothesis that intermittent rarity in the Pacific sardine is essentially determined by the sardine's weak invasibility in the fluctuating marine community.

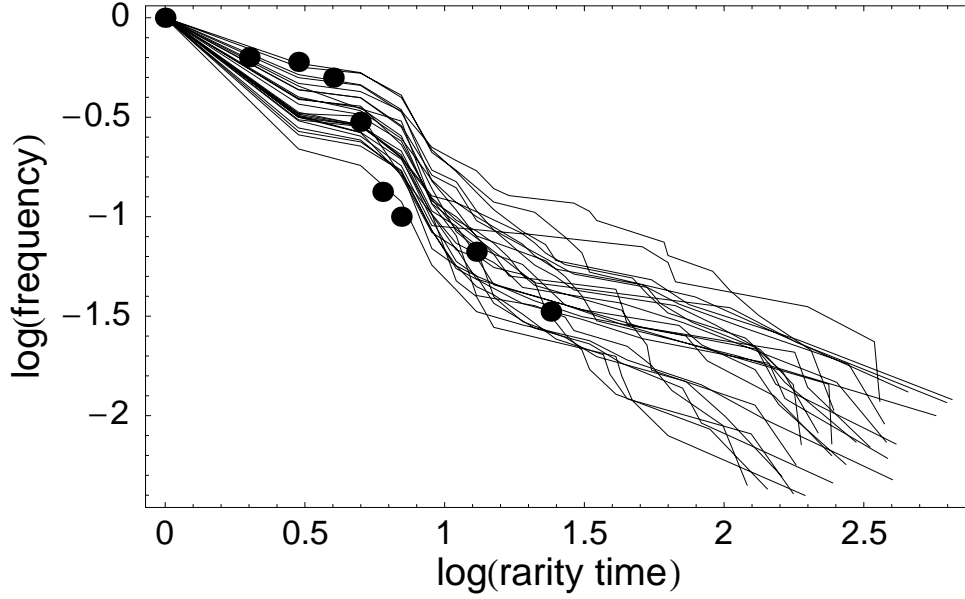


FIG. 10. Survival function of rarity times from short simulations of the Gatto model (plain lines) and from the Pacific sardine data shown in Fig. 1A (black circles). The survival function estimated at any t gives the frequency of rarity phases longer than t . Given that the distribution of rarity phases scales as $T^{-3/2}$, the survival function must scale as $t^{-1/2}$. The figure displays the survival functions computed from 25 runs of the Gatto model Eqs. (17) over 1,500 time steps.

Discussion

Intermittent rarity has been observed in species of prominent interest to population biologists, including various species under conservation efforts, harvested populations of fish and insect pests. The mechanisms that underlie intermittent rarity have remained poorly understood (Royama 1992, Rosenzweig and Molino 1997). Yet knowing the causes and processes that underlie intermittent rarity is needed to predict the natural occurrence and extent of recurrent episodes of low abundance with the aim of taking appropriate management decisions (Rosenzweig and Molino 1997).

The study of a prototypical community model and three purposely disparate two-species competition models has yielded two main results, that we discuss below.

(1) There needs not be any external factor (e.g. artificial release of competition or predation pressures, or immigration) for explaining the alternation of rarity and

commonness. Intermittent rarity develops in species that demonstrate weak invading abilities against a fluctuating background community.

(2) In spite of apparent irregularity through time, rarity phases are distributed according to a well-defined power law, which shows that intermittent rarity is a scale-free phenomenon. The scaling exponent of the power law is universal within the class of competition models considered here. Incorporating demographic stochasticity in the model shows that the distribution of rarity times changes predictably with the community carrying capacity.

Competition, fluctuations and intermittent rarity

After Vandermeer (1993) who reported the occurrence of intermittent rarity in two coupled resource-consumer systems, our results show that similar extreme population fluctuations can arise from the simplest competitive interactions. The background community operates as a slaving system for the intermittently rare species. This endogeneous forcing generates significant variations in the instantaneous invasion exponent of the rare species, through both positive and negative values, begetting a decline into arbitrarily long periods of scarcity followed by bursts of abundance. Fluctuations in the background community may be random (environmental noise superimposed on the background community steady state or cycle) or deterministic (when the background community settles on a strange attractor). In the latter case, the whole community (including the intermittently rare species) is chaotic.

Other mechanisms for chaotic outbreaks have been documented from the study of periodically-forced epidemiological and predator-prey models (e.g., Olsen and Schaffer 1990, Rinaldi et al. 1993, Gagnani and Rinaldi 1995), and models of tri-trophic food chains (e.g., Hastings and Powell 1991, De Feo and Rinaldi 1997). All of these models involve the coupling of several subsystems, each of them exhibiting periodic oscillations on its own. If the oscillation frequencies of the different subsystems are incommensurate, then chaos may develop; if in addition the frequencies are of very different orders of magnitude, meaning that the subsystems

oscillate on very different timescales, the system dynamics may exhibit long laminar phases (Muratori and Rinaldi 1992). Important differences with our description of intermittent rarity include: (i) In these models, laminar phases need not be phases of rarity. (ii) The conditions for intermittent rarity do not require that the rare species be oscillating should it be isolated from the background community. (iii) In models giving rise to intermittent rarity, the occurrence of long versus short rarity phases does not rely on timescale separation in the dynamics of different components of the system; short-term fluctuations in the instantaneous invasion exponent suffice to account for rarity phases of *any* duration.

Criticality and scaling exponents of intermittent rarity

It is remarkable that two-species competition models as disparate as the Gatto, Franke-Yakubu and Hochberg-Hawkins models all predict that irrespective to specific parameter values, the statistical distribution of rarity times in the limiting case of very large carrying capacity is a power law with scaling exponent close to $-3/2$. This is further in agreement with the analytical study of a prototypical model (Eq. [10] and Appendix 1).

The power law indicates that rarity dynamics have no characteristic timescale and that there are rarity phases of arbitrarily long length. There is « nothing special » about extremely long rarity phases, and no wild perturbations of the community are needed to produce them (Bak 1994). The smoothness of the power law, with the number of long rarity phases extending smoothly from the much larger number of short rarity events, shows that the same competition mechanism that governs short rarity episodes also governs long ones. The frequency of short rarity phases tells us the expected frequency of the long rarity phases.

How does the scaling dynamics found in two-species models apply to more complicated community structures? The theory of critical phenomena suggests that scaling exponents should depend most strongly upon gross features like the system symmetries and dimension (Baxter 1982, Stanley and Ostrowsky 1990, Stanley 1995).

In the ecological context, the proof of the $-3/2$ scaling in our prototypical model Eq. (10) is illuminating (see Appendix 1). The detailed calculations rely on the rare population being nonstructured and the background community being modelled as a one-dimensional density variable ($Y(t)$ in Eq. [10]). We can therefore conclude that the $-3/2$ exponent holds for any unstructured population that interacts with a background community which possesses an ergodic property (see Crowe 1997 for a review). Here ergodicity means convergence to a stable structure, irrespective to initial conditions (whereas densities may fluctuate cyclically or chaotically). Ergodicity applies when vital rates are all affected by the same density variable. Then the multidimensional community model boils down to a scalar nonlinear difference equation governing the dynamics of that single density variable (Cushing 1989, Crowe 1994, 1997).

When ergodicity does not hold, the background community will no longer be reducible to a one-dimensional system and the scaling exponent should be affected. The higher dimension of the community can then be estimated as the 'feedback environment dimension' (Metz et al. 1996, Heino et al. 1997, Meszéna and Metz *in press*). The feedback environment dimension measures the maximum number of interacting species which can be mutually invisable in the community. In practice, if the population densities settle on stable equilibria (no complex dynamics), then the feedback environment dimension is equal to the minimum number of variables needed to make the community's equations linear in the species densities (O. Diekmann, personal communication). We suggest that there may be a predictable relationship between the community dimension so defined and the scaling exponent of intermittent rarity.

Intermittent rarity and scaling: empirical evidence

Several harvested marine fish populations provide instances of intermittent rarity. Their dynamics have been reconstructed from fish scale-deposition records (Soutar and Isaacs 1974, DeVries and Pearcy 1982, Baumgartner et al. 1992). In sardines, one

of the best documented case, the alternation of phases of extreme rarity and phases of commonness are visible in data on several timescales: during the last century (see e.g. Cury 1988), across the past two millenia (Fig. 1A) and over the whole Holocene period (Fig. 1B). We analysed the largest data set (Fig. 1A) and found a remarkable agreement with the predicted $-3/2$ scaling. Weak invasibility in a fluctuating community may therefore offer a consistent explanation to the rarity phases observed in the Pacific sardine. As a competitor of the sardine, a serious candidate is the Northern anchovy *Engraulis mordax* (see Radowich 1981, Baumgartner et al. 1992). Food may be a limiting resource and a factor of interspecific competition at the critical time in the larval development when feeding first begins. The presence of the proper food of the right size at the right density in the vicinity of the larva should determine whether or not a larval anchovy or sardine survives past this critical stage. Intraspecific density-dependence involves cannibalism of eggs by sardines and anchovies (Radowich 1981). Furthermore, studies of fish debris from coastal upwelling off California (Soutar and Isaacs 1974) and Peru (DeVries and Pearcy 1982) showed that the anchovy has remained abundant through historical time in both ecosystems, though its density has been fluctuating widely on the three timescales mentioned above. The requirement for intermittent rarity that a species interacts with a fluctuating competitor seems to be met in the sardine-anchovy community.

Multispecies interactions may also explain intermittent rarity in the extensively studied spruce budworm outbreak processes (see Royama 1992, chapter 9, for a review). Royama (1992) argues that the theory of epicenters (seasonal climatic forcing and migration between local populations) is inoperative as budworm outbreaks are concerned. Budworm larval survival is not as sensitive to wheather conditions as the theory supposed. Also, moth dispersal may significantly enhance regional abundance only when the population has already entered a growing phase. Royama's alternative theory, based on a careful analysis of long-term data, emphasizes the role of density dependence (when defoliation becomes severe, the recruitment rate drops) and interactions with parasitoids. Our study gives support to

the view that such intra and interspecific factors may fully account for the recurrent epidemics and rarity phases experienced by the spruce budworm.

Implications for conservation and population management

The power law that governs intermittent rarity provides a useful way of estimating the likelihood, in a given interval of time, of a rarity phase of any given duration. When entering a rarity phase, the species viability becomes highly vulnerable to demographic stochasticity. We are currently studying general means of quantitatively predicting the extinction risk in periods of rarity. How small immigration may affect the distribution of rarity phases and the population viability is also a topic under current investigation.

The stochastic version of our model that incorporates demographic noise shows that intermittent rarity is not inconsistent with a large carrying capacity. Such large carrying capacities are typical of fish populations that undergo harvesting (e.g. Cury 1988), including the various species of rare sardines mentioned in this paper. Future work should address the effect of harvesting on the viability of intermittently rare species. Over-fishing, that was thought to be responsible for the Pacific sardine collapse a few decades ago, cannot explain the intermittent rarity of the fish over the past centuries. Rather counter-intuitively, the indiscriminate harvesting of a fish community may have little effect on intermittently rare species during their periods of scarcity, for the likelihood of them being affected by catches becomes negligible, whereas the removal of a substantial amount of competitors may facilitate recovery out of a rarity phase. In contrast, harvesting during times of abundance may hasten the opening of a rare episode, thereby increasing the overall extinction risk due to rarity phases.

An important further issue in the context of management of rare species is temporal concordance (e.g., McGowan and Walker 1985, Rahel 1990, Gaston 1994), a notion that has received little theoretical attention so far. Our modelling framework could be extended to include more than one intermittently rare species and to

examine conditions on the community structure for the synchronized development of rarity phases in different species.

Concluding remarks

A remarkable consequence of scaling and criticality is that predictions of even highly idealized models can be used to describe real systems accurately (Stanley 1995). This is especially desirable in biology, as we require models that give robust dynamical behavior without the need to adjust parameters to exact values. In physics, the universality property of critical phenomena has been demonstrated recently by Back et al. (1995) who experimentally tested the scaling dynamics of the Ising model (which describes ferromagnetic interactions). Although the details of the system they studied did not perfectly mirror the conditions of the model, the measured scaling exponent strikingly conformed to the calculated result. The key here is that the model, in spite of its caricatural nature, retains the essential symmetry and dimensionality properties of the physical process.

In the ecological perspective, critical phenomena and power laws have been documented in the spatio-temporal dynamics of epidemics of communicable diseases, both in models (Rhodes and Anderson 1996a) and in real populations (Rhodes and Anderson 1996b); and in the dynamics of bird communities (Keitt and Stanley 1998). Here we suggest that even crude information on the community structure might be sufficient to estimate the scaling exponent of the dynamics of intermittently rare species, thereby facilitating predictions of relevance for population management and conservation. Conversely, when population time series showing intermittent rarity are available, one can measure scaling exponents directly from them. This might offer a new way of getting insights into the structure of communities of interacting species, for we expect the scaling exponent of an intermittently rare species to reflect the dimension of the community to which it belongs. Predicting the quantitative relationship between the scaling exponent of rarity dynamics and community dimension is a challenging problem that urgently needs to be tackled by theoretical ecologists.

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Appendix 1

Heagy et al.'s (1994) and Venkataramani et al.'s (1995, 1996) have carried out extensive mathematical studies of 'on-off intermittency', an aperiodic switching between laminar behavior and bursts of oscillations that arise in a large number of physical phenomena. Their results can be used straightforwardly to prove the existence of a $-3/2$ power law in the dynamics of intermittent rarity governed by our prototypical model Eq. (10). Here we outline the main steps of such a proof.

During a rarity phase, the rare species dynamics are 'slaved' by the density of the common population. Thus, in first approximation, $X(t)$ follows the recursion equation $X(t+1) = e^{\chi(t)} X(t)$. To capture the basic features of intermittent rarity one may choose $\chi(t)$ to be any stochastic process with a small positive mean χ and non-zero variations about the mean so that $\chi(t)$ is sometimes negative. To satisfy these requirements, we construct the process $\chi(t)$ given by $-\alpha$ with probability p and $+\alpha$ with probability $1-p$ where $p < 1/2$. Then the invasion exponent is $\chi = (1-2p)\alpha$. The pivotal argument to derive the scaling property of rarity times is that as χ goes to zero, the set Θ of time intervals when the rare species experiences densities above a given threshold approaches a fractal if time is rescaled appropriately. More precisely, let us choose the rarity threshold equal to 1 and rescale time by defining $\tau = (1-2p)^2 t$. We then let p goes to $1/2$ and look at the process in the range $0 \leq \tau \leq 1$. If $B(\delta)$ denotes the number of 'boxes' of length δ required to cover Θ , a random walk argument developed by Venkataramani et al.'s (1996) shows that the distribution of $B(\delta)$ is a power law with exponent $-1/2$, which means that Θ is fractal. The random walk description of the process $X(t)$ is based on defining $u(t) = -\ln X(t)/\alpha$. For appropriate choice of $X(0)$, the process $u(t)$ will take on integer values. If one sets an absorbing boundary at 0 (which corresponds to $X = 1$), then $u(t)$ is a random walk on the line of integers with a one-step increment to the

right with probability p if $u(t) > 0$. Then one can write recursion equations for the probability $\pi(l, t)$ that $u(t) = l$, from which one can calculate the probability of being absorbed in any given number of steps. $B(\delta)$ is then equal to this probability divided by δ , given that the total number of intervals of length δ in the interval $0 \leq \tau \leq 1$ is $1/\delta$. We emphasize that the random walk argument used here critically relies on the assumption that the intermittently rare process $X(t)$ is one-dimensional.

The calculations go on by introducing the probability $b(\delta)$ that $X(t)$ experience one burst in any (rescaled) time interval of length δ given that $X(t)$ burst once in the previous contiguous interval of length δ . One can look at $b(\delta)$ in two ways. First, $b(\delta)$ and $B(\delta)$ are related by

$$(A-1) \quad B(2\delta) = B(\delta)[1 - b(\delta)],$$

for successive bursts in any pair of consecutive intervals of length δ will require two boxes in a cover by intervals of length δ , but only one box in a cover by intervals of length 2δ . Second, $b(\delta)$ is the conditional probability of having a rarity phase of (rescaled) length between δ and 2δ given that there is a rarity phase longer than δ . If $q(\delta)$ denotes the probability of having a rarity phase longer than δ , then one obtains

$$(A-2) \quad b(\delta) = [q(\delta) - q(2\delta)]/q(\delta).$$

Thus, $q(\delta)$ can be derived from $b(\delta)$ which can itself be derived from $B(\delta)$. We obtain $b(\delta) = 1 - 1/\sqrt{2}$ from Eq. (A-1), which combines with (A-2) to yield $q(2\delta)/q(\delta) = 1/\sqrt{2}$, hence

$$(A-3) \quad q(\delta) = q_0 \delta^{-1/2}$$

where q_0 is a constant. If $P(T)$ is the probability of having a rarity phase of (unscaled) length T , we must have

$$(A-4) \quad q(\delta) = \sum_{\text{int}[\delta/(1-2p)^2]}^{+\infty} P(T).$$

The series is absolutely convergent, hence

$$(A-5) \quad q(\delta) \approx \int_{\delta/(1-2p)^2}^{+\infty} P(T) dT$$

which, together with (A-3), leads to $P(T) \propto T^{-3/2}$.

Appendix 2

The Hochberg-Hawkins model Eqs. (23) assumes that hosts experience two sources of refuge from parasitoid attack: spatial heterogeneity and complete invulnerability in specific structural refuges. Generations are discrete and non-overlapping. During each generation, a proportion of the larval host community is vulnerable to parasitism. The parasitoid is assumed to be a generalist species whose density is maintained at a constant level by other host species in addition to the two host species considered here. The difference equations, constituting the density $X_1(t)$ and $X_2(t)$ of hosts, are given by Eqs. (23). Maynard-Smith density dependence (Maynard Smith 1974) is used to model the proportion d of hosts surviving from intra and interspecific competition:

$$(A.1) \quad d[X_1(t), X_2(t)] = \left\{ 1 + [X_1(t)(f_1 - 1)/Q + X_2(t)(f_2 - 1)/Q]^c \right\}^{-1},$$

where Q is the carrying capacity of the host community and c refers to individual competitive ability, the same for both host species. The functional response of parasitoids, g , is given by

$$(A.2) \quad g[X_1(t), X_2(t)] = \left\{ 1 + \frac{aG[X_1(t), X_2(t)]}{k[1 + a(f_1 X_1(t)(1 - \alpha_1) + f_2 X_2(t)(1 - \alpha_2))/\eta]} \right\}^{-k}$$

Here, a is the per capita searching efficiency of the parasitoids; h is the maximum number of hosts that a single parasitoid individual may attack in a given generation; k is the clumping parameter of the negative binomial distribution of parasitoid search (with small values of k signalling increased heterogeneity); and

$$(A.3) \quad G[X_1(t), X_2(t)] = h \left\{ 1 - \exp\left[-(f_1 X_1(t)(1 - \alpha_1) + f_2 X_2(t)(1 - \alpha_2))/b\right] \right\},$$

with h the maximum number of parasitoids attacking and b a constant, is the actual number of parasitoids that launch attacks on the hosts concerned here (see Hochberg and Hawkins 1992).