

## Random Perturbations of Dynamical Systems with Absorbing States\*

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**Abstract.** Let  $F : M \rightarrow M$  be a continuous dissipative map of a separable metric space  $M$ . Consider a finite collection  $\mathcal{A}$  of closed  $F$ -forward invariant sets that is closed under intersection and that contains  $M$ . For all  $\epsilon > 0$ , let  $X^\epsilon$  be a Markov chain for which the elements of  $\mathcal{A}$  are absorbing (e.g., extinction boundaries for a population, genotype, or strategy) and such that  $d(X_{t+1}^\epsilon, F(X_t^\epsilon)) \leq \epsilon$  for all  $t$ . Under an additional nondegeneracy condition (i.e., the noise extends locally in all nonabsorbing directions) and a continuity-like condition on the supports of the random perturbations, we show that for sufficiently small values of  $\epsilon$ ,  $X^\epsilon$  asymptotically spends all of its time near certain invariant sets of  $F$ , so-called absorption preserving chain attractors. Moreover, the weak\* limit points of  $X^\epsilon$ 's stationary distributions as  $\epsilon \rightarrow 0$  are  $F$ -invariant probability measures whose supports lie in the absorption preserving chain attractors. Applications to the dynamics of structured and unstructured populations, multispecies interactions, and evolutionary games are given.

**Key words.** random perturbations of dynamical systems, chain recurrence, absorbing sets, ecological and evolutionary dynamics

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**1. Introduction.** The evolution of many physical and biological processes is governed by a mixture of stochastic forces and nonlinear determinism. For example, ecological and evolutionary systems involve nonlinear interactions that are constantly subject to environmental and demographic fluctuations [1, 17]. When nonlinear determinism dominates, the evolution of these processes is often described by nonlinear dynamical systems in which the current state of the system determines all future states [5]. For these deterministic approximations, it is natural to ask about the correspondence between the behavior of the unperturbed dynamical system and the same system subject to small random perturbations [13]. This correspondence was studied initially in 1933 by Pontryagin, Andronov, and Vitt [15], and more recently by Wentzell and Freidlin [6, 18], Ruelle [16], and Kifer [12]. Each of these studies was primarily motivated by physical processes in which the random perturbations could act locally in all directions of the state space. In many biological systems, however, stochastic forces are limited by biological constraints. These constraints create “absorbing sets” in the state space, which the system cannot leave after entering. For instance, in a closed ecological community

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a species that goes extinct remains extinct. It cannot be resurrected by stochastic forces. Alternatively, in structured community models random perturbations may affect the number of individuals in each of the classes or stages, but may not change the structural state or parameters of each of the individuals. Depending on the structure of the model, the collection of absorbing sets may be large or small. For a semelparous population model with age structure, a population missing one or more classes always has one or more age classes missing, a fact that should be respected by random perturbations. For example, the absence of the reproducing age class in the current generation results in the absence of the youngest age class in the next generation. On the other hand, for most iteroparous population models the only absorbing set is extinction [3, 14, 19].

The goal of this article is to investigate random perturbations of dynamical systems with these types of absorbing sets. To achieve this goal, we introduce in section 2 the notion of an *absorbing  $\pi$ -system*, i.e., a collection of closed forward invariant subsets closed under intersection, and random  $\epsilon$ -perturbations of deterministic maps that preserve a given absorbing  $\pi$ -system. These random  $\epsilon$ -perturbations act after the deterministic map, preserve the elements of the absorbing  $\pi$ -system (i.e., once the process enters an absorbing set, it remains in that absorbing set), and are no larger than  $\epsilon > 0$  in size with respect to a given metric on the community state space. We illustrate these definitions with ecological models accounting for demographic, environmental, and migrational stochasticity, with replicator equations accounting for demographic, environmental, and mutational stochasticity, and with an age-structured model. To describe the asymptotic behavior of the randomly perturbed system, we prove in section 3 the existence of invariant probability measures  $\mu^\epsilon$  whenever the unperturbed system has at least one attractor. These invariant probability measures describe the long-term statistical behavior of trajectories of the randomly perturbed system. As  $\epsilon \downarrow 0$ , the work of Khasminskii [11] (see also Kifer [12]) implies that the limit points of these invariant probability measures are invariant probability measures for the unperturbed system. These limit points are *natural invariant measures* for the unperturbed system, as when  $\epsilon > 0$  is sufficiently small the long-term statistical behavior of the perturbed system is well approximated by these natural invariant measures.

Since the unperturbed system may have several invariant measures, including ones supported by repellers, sections 4 and 5 determine which invariant sets of the unperturbed system can actually support the natural invariant measures. In section 4 we introduce the notion of an absorption preserving chain attractor. This generalizes the notion of extinction preserving chain attractor as presented in Jacobs and Metz [10], which in turn is a generalization of the concept of chain attractor as derived by Ruelle [16]. Ruelle introduced chain attractors to describe the asymptotic behavior of physical systems, in which the dynamics inherently is influenced by small disturbances. In his construction of chain attractors Ruelle used so-called *pseudo-orbits* to model the effect of limited noise on the orbits of an unperturbed system. In [10] his approach is adapted to unstructured, and in [7] to structured, community-dynamical models as they are studied in ecology, leading to the notion of extinction preserving chain attractors. The present paper extends these ideas to absorbing  $\pi$ -systems that can account for a greater variety of stochastic influences as outlined above. In section 5 we prove that under appropriate assumptions the natural invariant measures are supported by the absorption preserving chain attractors. Moreover, under additional assumptions and  $\epsilon > 0$  sufficiently small,

the randomly  $\epsilon$ -perturbed system eventually remains near *one* of the absorption preserving chain attractors of the unperturbed system.

To illustrate the utility of the theory, we apply our results in section 6 to models of competing species and replicator dynamics. The addition of noise in these models is proven to have significant effects. In section 7 we make some concluding remarks about our results and pose some open questions.

**2. Definitions and examples.** Let  $M$  be a separable metric space with metric  $d$ , and  $F : M \rightarrow M$  a continuous map. Given  $A \subset M$  and  $x \in M$ , let  $\text{dist}(x, A) = \inf\{d(x, y) : y \in A\}$ , and for  $\delta \geq 0$  let  $N(A, \delta) = \{y \in M : \text{dist}(y, A) \leq \delta\}$ . For notational convenience, when  $A = \{x\}$  we write  $N(x, \delta)$  instead of  $N(\{x\}, \delta)$ . We recall a few definitions from dynamical systems theory. Given a subset  $S \subset M$ , define  $F^n(S) = \{F^n(x) : x \in S\}$  and  $\omega(S) = \bigcap_{n>0} \overline{\bigcup_{m \geq n} F^m(S)}$ , with the notational adaptation to  $\omega(x)$  in the case  $S = \{x\}$ . A set  $A \subset M$  is *F-forward invariant* if  $F(A) \subset A$ , and *F-invariant* if  $F(A) = A$ . A compact set  $A \subset M$  is an *attractor for F* if there exists a compact neighborhood  $U$  of  $A$  such that  $\omega(U) = A$ . The *basin of attraction* of a compact  $F$ -invariant set  $A \subset M$  is the set of points  $x \in M$  such that  $\omega(x) \subset A$ . A point  $x \in M$  is *recurrent for F* if  $x \in \omega(x)$ .

For the map  $F$ , specific forward invariant sets may be viewed as absorbing under stochastic perturbations of  $F$ . In population models, for example, these forward invariant sets may correspond to the extinction of one or more species, subpopulations, phenotypes, or genotypes. To allow for a mathematical framework flexible enough for structured and unstructured ecological models, replicator equations, and hybrids of these models, we make the following definitions.

**Definition 1.** An absorbing  $\pi$ -system for  $F$  is a finite collection  $\mathcal{A}$  of closed  $F$ -forward invariant subsets of  $M$  which includes the set  $M$  and which is closed under intersection (i.e.,  $A, B \in \mathcal{A}$  implies that  $A \cap B \in \mathcal{A}$ ). An element of  $\mathcal{A}$  is called an absorbing set.

**Definition 2.** For  $x \in M$  define the minimal absorbing set for  $x$ , denoted  $\mathcal{A}^*(x)$ , to be the smallest element in  $\mathcal{A}$  containing  $x$ .

**Definition 3.** For any set  $A \subset M$  and  $\delta \geq 0$  define the  $\delta$ -neighborhood of  $A$  as

$$N_{ap}(A, \delta) = \bigcup_{x \in A} N(x, \delta) \cap \mathcal{A}^*(x).$$

The index *ap* refers to absorption preservation. For notational convenience we write  $N_{ap}(x, \delta)$  instead of  $N_{ap}(\{x\}, \delta)$ .

For a given map  $F : M \rightarrow M$  there are many potential choices of an absorbing  $\pi$ -system, corresponding to different choices about how random perturbations affect the system. Assuming that a  $\pi$ -system  $\mathcal{A}$  has been chosen, we make the following definition.

**Definition 4.** For  $\epsilon \geq 0$ , a random  $\epsilon$ -perturbation of  $F$  respecting the absorbing  $\pi$ -system  $\mathcal{A}$  is a (discrete time) Markov chain  $X^\epsilon$ , taking values in  $M$  and with transition kernel  $P_x^\epsilon$ ,

$$P_x^\epsilon(\Gamma) = P(X_{t+1}^\epsilon \in \Gamma | X_t^\epsilon = x) \quad \text{for all } x \in M \text{ and for all Borel subsets } \Gamma \subseteq M,$$

which satisfies

$$\text{H1. } P_x^\epsilon(N_{ap}(F(x), \epsilon)) = 1.$$

**H1** ensures that the forward invariant sets in  $\mathcal{A}$  are absorbing for  $X^\epsilon$  and that random  $\epsilon$ -perturbations are  $\epsilon$  small. When  $\mathcal{A} = \{M\}$ , we recover random perturbations considered by Kifer [12] and Ruelle [16].

To illustrate choices of random  $\epsilon$ -perturbations that satisfy **H1**, we introduce several examples. In these examples, if  $X_t^\epsilon$  is a vector, then  $X_{t,i}^\epsilon$  denotes the  $i$ th component of  $X_t^\epsilon$ .

**2.1. Ecological equations.** Consider  $M$  given by  $\mathbf{R}_+^k = \{x = (x_1, \dots, x_k) \in \mathbf{R}^k : x_i \geq 0\}$ , where  $x = (x_1, \dots, x_k)$  is the vector of population densities. Let  $d(x, y) = \max_i |x_i - y_i|$ . If  $f_i(x)$  denotes the per capita growth rate of the  $i$ th population, then  $F(x) = (x_1 f_1(x), \dots, x_k f_k(x))$  defines an *ecological difference equation*. For the sake of simplicity, we assume that there exists  $\xi \geq 1$  such that  $F(\mathbf{R}_+^k) \subset [0, \xi]^k$  (i.e.,  $F$  is a compact map). For this map we illustrate three choices of noise, corresponding to environmental, demographic, and immigration stochasticity. Combinations of these noises result in different choices of absorbing  $\pi$ -systems.

**Environmental stochasticity.** Environmental stochasticity occurs when random fluctuations in the environment result in random fluctuations in reproductive or mortality rates. Let  $\{Z_t\}_{t \geq 0}$  be a sequence of independent random vectors taking values in  $[-1/\xi, 1/\xi]^k$ . Let  $Z_{t,i}$  denote the  $i$ th component of  $Z_t$ . Define a random  $\epsilon$ -perturbation  $X^\epsilon$  of  $F$  by

$$X_{t+1,i}^\epsilon = (1 + \epsilon Z_{t,i}) F_i(X_t^\epsilon).$$

Since  $|(1 + \epsilon Z_{t,i}) F_i(X_t^\epsilon) - F_i(X_t^\epsilon)| = \epsilon |Z_{t,i} F_i(X_t^\epsilon)| \leq \epsilon$ , this choice of  $X^\epsilon$  satisfies **H1** with respect to the absorbing  $\pi$ -system generated by  $M$  and all finite intersections of the sets  $\{x \in \mathbf{R}_+^k : x_i = 0\}$ .

**Demographic stochasticity.** Demographic stochasticity is the effect that the randomness of birth and death processes has on finite populations. Let  $\gamma \gg 1$  denote the habitat size,  $N_i = x_i \gamma$  the abundance of population  $i$ ,  $d_i = d_i(\epsilon) \in (0, 1)$  the probability that an individual of population  $i$  dies, and  $f_i(x)/(1 - d_i)$  the number of progeny produced per individual of population  $i$ . If reproduction is deterministic and followed by independent stochastic deaths, the number of surviving individuals of population  $i$  is given by a binomial random variable with mean  $(1 - d_i) N_i f_i(x)/(1 - d_i) = N_i f_i(x)$  and standard deviation  $\sqrt{d_i N_i f_i(x)}$ . If we approximate these binomials by appropriately truncated normal random variables  $Z_{t,i}(x)$ , then  $X_{t+1,i}^\epsilon = F_i(X_t^\epsilon) + Z_{t,i}(X_t^\epsilon)$ ,  $i = 1, \dots, k$ , satisfies **H1** with respect to the absorbing  $\pi$ -system generated by  $M$  and all finite intersections of the sets  $\{x \in \mathbf{R}_+^k : x_i = 0\}$ .

**Immigration stochasticity.** Suppose that a subset of populations  $I \subset \{1, \dots, k\}$  receives a random influx of immigrants. To model this, let  $\{Z_t\}_{t \geq 0}$  be a sequence of random vectors with support in  $[0, 1]^k$ . For populations  $i \notin I$  we assume that  $Z_{t,i} = 0$ , i.e., no immigrants. The random  $\epsilon$ -perturbation of  $F$  given by  $X_{t+1}^\epsilon = F(X_t^\epsilon) + \epsilon Z_t$  satisfies **H1** with respect to the absorbing  $\pi$ -system generated by  $M$  and all finite intersections of the sets  $\{x \in \mathbf{R}_+^k : x_i = 0\}$  for  $i \notin I$ .

**Combined random perturbations.** In addition to the random perturbations mentioned above, combinations of these random perturbations (e.g., demographic and environmental stochasticity) will also satisfy **H1** with respect to the appropriate absorbing  $\pi$ -system.

**2.2. Replicator difference equations.** Consider  $M = \{x \in \mathbf{R}_+^k : \sum_{i=1}^k x_i = 1\}$ , where  $x = (x_1, \dots, x_k)$  is the vector of strategy frequencies. Let  $d(x, y) = \max_i |x_i - y_i|$ . If  $f_i(x)$  is the relative fitness of the  $i$ th strategy, then

$$F(x) = \left( \frac{x_1 f_1(x)}{\sum_j x_j f_j(x)}, \dots, \frac{x_k f_k(x)}{\sum_j x_j f_j(x)} \right)$$

defines the distribution of strategies in the next generation, and is called a *replicator equation* (see, e.g., [9]).

**Environmental and demographic stochasticity.** These forms of random perturbations can be developed for replicator equations in a manner similar to the ecological equations.

**Random mutations.** Imagine that for every strategy  $i \in \{1, \dots, k\}$  there is a collection of strategies  $I_i \subset \{1, \dots, k\}$  that randomly mutate to strategy  $i$ . We assume that  $I_i$  always includes  $i$ . Let  $\{Z_t(i, j)\}_{t \geq 0}$  be a sequence of independent random variables that represent the fraction of strategy  $i$  individuals that mutate to strategy  $j$  at time  $t$ . For each  $t \geq 0$  we require  $Z_t(i, j) \geq 0$ ,  $\sum_{j=1}^k Z_t(i, j) = 1$ , and  $Z_t(j, i) > 0$  if and only if  $j \in I_i$ . Define  $X^\epsilon$  by

$$X_{t+1, i}^\epsilon = \frac{\sum_{j \in I_i} Z_t(j, i) X_{t, j}^\epsilon f_j(X_t^\epsilon)}{\sum_{j=1}^k X_{t, j}^\epsilon f_j(X_t^\epsilon)}.$$

Under the assumption that  $Z_t(i, j) \leq \frac{\epsilon}{k-1}$  for all  $i, j \in \{1, \dots, k\}$  and  $i \neq j$ ,  $X^\epsilon$  satisfies H1 with respect to the absorbing  $\pi$ -system generated by  $M$  and the sets  $\{x \in M : x_j = 0 \text{ for all } j \in I_i\}$  with  $i = 1, \dots, k$ .

**2.3. Age-structured populations.** Consider a population with  $k$  age classes. Let  $x = (x_1, \dots, x_k)$  be the population vector, where  $x_i$  is the density of age class  $i$ . A standard model (see, e.g., [2]) for this population is a nonlinear Leslie matrix model

$$F(x) = \begin{pmatrix} f_1(x) & f_2(x) & f_3(x) & \dots & f_{k-2}(x) & f_{k-1}(x) & f_k(x) \\ s_1(x) & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & s_2(x) & 0 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & s_{k-1}(x) & 0 \end{pmatrix} x,$$

where  $f_i$  is the mean number of progeny produced per generation by an individual in age class  $i$ , and  $s_i$  is the probability that an individual survives from age class  $i$  to age class  $i + 1$ . For an age-structured model one can add demographic, environmental, and immigrational stochasticity to each of the age classes. For instance, demographic stochasticity via truncated normal approximations can be used to represent variability in survivorship between age classes and variability in fecundities within each reproductive age class. Depending on the number of reproductive age classes, demographic stochasticity can result in different forms of absorbing  $\pi$ -systems. For example, if the population is semelparous with  $f_1 = f_2 = \dots = f_{k-1} = 0$  and  $f_k \neq 0$ , then the natural absorbing  $\pi$ -system is given by  $M$ ,  $\cup_i \{x \in \mathbf{R}_+^k : x_i = 0\}$ ,  $\cup_{i_1 > i_2} \{x \in \mathbf{R}_+^k : x_{i_1} = x_{i_2} = 0\}, \dots, \{0\}$ . Alternatively, if the population is significantly iteroparous, e.g.,  $f_i > 0$  for all  $i$ , then the natural absorbing  $\pi$ -system consists of  $M$  and  $\{0\}$ .

**3. Empirical and natural invariant measures.** Given  $X^\epsilon$ , define for  $t \geq 1$  the *empirical measures*  $\nu_t^\epsilon$  by

$$\nu_t^\epsilon = \frac{1}{t} \sum_{i=1}^t \delta_{X_i^\epsilon},$$

where  $\delta_x$  is a Dirac measure based at the point  $x \in M$ . One can think of empirical measures as corresponding to plotting a single pixel at each of the points  $X_1^\epsilon, \dots, X_t^\epsilon$ , for increasing values of  $t$ . As one continues to plot these pixels, certain regions of the phase space  $M$  get darkened more than other regions of the phase space. To describe the limiting picture, we consider *weak\* limit points* of the sequence  $\nu_1^\epsilon, \nu_2^\epsilon, \nu_3^\epsilon, \dots$ . To define a weak\* limit point, consider any continuous function  $h : M \rightarrow \mathbf{R}$ . The average of this function with respect to  $\nu_t^\epsilon$  is the average observed value of  $h$  up to time  $t$ :

$$\int_M h(x) d\nu_t^\epsilon(x) = \frac{1}{t} \sum_{i=1}^t h(X_i^\epsilon).$$

A weak\* limit point of the sequence  $\nu_1^\epsilon, \nu_2^\epsilon, \dots$  is a Borel probability measure  $\mu^\epsilon$  such that there exists an increasing sequence of times  $\{t_n\}_{n=1}^\infty$  satisfying

$$\lim_{n \rightarrow \infty} \frac{1}{t_n} \sum_{i=1}^{t_n} h(X_i^\epsilon) = \int_M h(x) d\mu^\epsilon(x)$$

for all bounded continuous functions  $h : M \rightarrow \mathbf{R}$ .

As we show below, these limit points  $\mu^\epsilon$  are often invariant measures for  $X^\epsilon$ , i.e., for every Borel set  $\Gamma \subset M$ ,

$$(1) \quad \int_M P_x^\epsilon(\Gamma) d\mu^\epsilon(x) = \mu^\epsilon(\Gamma).$$

In the special case of  $\epsilon = 0$ , (1) simplifies to

$$\mu^0(F^{-1}(\Gamma)) = \mu^0(\Gamma),$$

and  $\mu^0$  is an *invariant measure* of  $F$ . Another means of defining an invariant measure for  $X^\epsilon$  is to introduce the operator  $\mathcal{P}_\epsilon^*$  on the space of probability measures:

$$\mathcal{P}_\epsilon^*(\mu)(\Gamma) = \int_M P_x^\epsilon(\Gamma) d\mu(x),$$

where  $\mu$  is a Borel probability measure and  $\Gamma$  is a Borel subset of  $M$ . An invariant measure  $\mu$  for  $X^\epsilon$  is just a fixed point of  $\mathcal{P}_\epsilon^*$ , i.e.,  $\mathcal{P}_\epsilon^*(\mu) = \mu$ . The importance of this invariance lies in the fact that when  $\epsilon > 0$  is sufficiently small, the invariant measures  $\mu^\epsilon$  for  $X^\epsilon$  obtained as weak\* limit points of the sequence  $\{\nu_t^\epsilon\}_{t \geq 1}$  will be well approximated by invariant measures of  $F$ . In particular, this will mean that if  $\epsilon > 0$  is sufficiently small,  $X^\epsilon$  will spend most of its time near the supports of specific invariant measures of  $F$ . Recall that the *support of a probability measure*  $\mu$ , denoted  $\text{supp}(\mu)$ , is the intersection of all closed sets  $K$  with  $\mu(K) = 1$ .

**Theorem 1.** Let  $F : M \rightarrow M$  be a continuous map,  $\mathcal{A}$  an absorbing  $\pi$ -system for  $F$ , and  $X^\epsilon$  a random  $\epsilon$ -perturbation of  $F$  respecting  $\mathcal{A}$ . Assume that  $A \in \mathcal{A}$  and that  $B$  is an attractor for  $F|_A$ . If  $X_0^\epsilon$  lies in the basin of attraction of  $B$ , then for  $\epsilon \geq 0$  sufficiently small the sequence  $\nu_1^\epsilon, \nu_2^\epsilon, \nu_3^\epsilon, \dots$  has (with probability one) weak\* limit points. These limit points are invariant measures for  $X^\epsilon$ , with support in  $B$ 's basin of attraction.

*Remark.* Recall that  $F : M \rightarrow M$  is *dissipative* if it admits a compact global attractor. Theorem 1 ensures the existence of invariant measures for random perturbations  $X^\epsilon$  of a dissipative  $F$  whenever  $\epsilon \geq 0$  is sufficiently small.

*Proof.* By H1 it suffices to prove the theorem when  $\mathcal{A} = \{M\}$ . Consequently, suppose that  $B \subset M$  is an attractor for  $F$  and that  $x \in M$  is in the basin of attraction of  $B$ . Assume that  $X_0^\epsilon = x$ . Let  $V$  be a compact neighborhood of  $B$  such that  $V$  is contained in  $B$ 's basin of attraction, and such that  $F(V)$  is contained in the interior of  $V$ . Since  $B$  is an attractor, there exists a natural number  $T$  such that  $F^T(x)$  is contained in the interior of  $V$ . By continuity of  $F$  there exists an  $\epsilon_1 > 0$  such that if  $x_0 = x, x_1, \dots, x_T \in M$  satisfy  $d(x_i, F(x_{i-1})) \leq \epsilon_1$  for  $i = 1, \dots, T$ , then  $x_T$  is contained in the interior of  $V$ . In particular, if  $\epsilon \leq \epsilon_1$ , then  $X_T^\epsilon$  is contained in the interior of  $V$  with probability one. Choose  $\epsilon_2 \in (0, \epsilon_1)$  such that  $N(F(V), \epsilon_2) \subset V$ . Define

$$U = \bigcup \{x_0 = x, \dots, x_T : d(x_i, F(x_{i-1})) \leq \epsilon_2 \text{ for } i = 1, \dots, T\}.$$

Our choice of  $\epsilon_2$  implies that, with probability one,  $X_t^\epsilon \in U \cup V$  for all  $t \geq 0$  and  $\epsilon \in [0, \epsilon_2)$ . Hence, for  $\epsilon \in [0, \epsilon_2)$  the empirical measures  $\nu_t^\epsilon$ ,  $t \geq 1$ , with probability one are supported by the compact set  $U \cup V$ . By weak\* compactness of the Borel probability measures supported in  $U \cup V$ , there exists a weak\* limit point  $\mu^\epsilon$  of the sequence  $\{\nu_t^\epsilon\}_{t \geq 1}$  as  $t \rightarrow \infty$ .

To see the invariance of this weak\* limit point, let  $h : M \rightarrow \mathbf{R}$  be any continuous and bounded function. Let  $\mathcal{F}_t$  denote the  $\sigma$ -algebra generated by  $X_1^\epsilon, \dots, X_t^\epsilon$ . Define sequences  $\{Y_t\}_{t \geq 1}$  and  $\{Z_t\}_{t \geq 1}$  by

$$Y_t = \frac{1}{t} (h(X_t^\epsilon) - E[h(X_t^\epsilon) | X_{t-1}^\epsilon])$$

and

$$Z_t = \sum_{i=1}^t Y_i.$$

$\{Z_t\}_{t \geq 1}$  is a martingale with respect to  $\{\mathcal{F}_t\}_{t \geq 1}$ , as

$$\begin{aligned} E[Z_{t+1} - Z_t | \mathcal{F}_t] &= E[Y_{t+1} | \mathcal{F}_t] \\ &= \frac{1}{t+1} (E[h(X_{t+1}^\epsilon) | \mathcal{F}_t] - E[h(X_{t+1}^\epsilon) | \mathcal{F}_t]) = 0. \end{aligned}$$

Let  $\|h\| = \sup_{x \in M} |h(x)|$ . Since  $E[Y_{t+1} | \mathcal{F}_t] = 0$ , we get that

$$\begin{aligned}
\left| E[Z_{t+1}^2] \right| &= \left| E \left[ \left( \sum_{i=1}^{t+1} Y_i \right)^2 \right] \right| \\
&= \left| E \left[ \sum_i Y_i^2 + 2 \sum_{i>j} Y_i Y_j \right] \right| \\
&= \left| \sum_i E[Y_i^2] + 2 \sum_{i>j} E[E[Y_i Y_j | \mathcal{F}_{i-1}]] \right| \\
&= \left| \sum_i E[Y_i^2] + 2 \sum_{i>j} E[Y_j E[Y_i | \mathcal{F}_{i-1}]] \right| \\
&= \left| \sum_i E[Y_i^2] \right| = \left| \sum_i E \left[ \frac{1}{i^2} (h(X_i^\epsilon) - E[h(X_i^\epsilon) | \mathcal{F}_{i-1}])^2 \right] \right| \\
&\leq \sum_{i=1}^{t+1} \frac{1}{i^2} 4 \|h\|^2.
\end{aligned}$$

Hence,  $\{Z_t\}_{t \geq 1}$  is an  $L^2$  martingale, and Doob's convergence theorem implies that  $\lim_{t \rightarrow \infty} Z_t$  converges with probability one. By Kronecker's lemma,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \sum_{i=1}^t (h(X_i^\epsilon) - E[h(X_i^\epsilon) | \mathcal{F}_{i-1}]) = 0$$

with probability one. Now suppose that  $\lim_{i \rightarrow \infty} \nu_{t_i}^\epsilon$  converges weakly to  $\mu^\epsilon$ . The previous estimate implies that

$$\begin{aligned}
\int h(x) d\mu^\epsilon(x) - \int h(x) d\mathcal{P}_\epsilon^*(\mu^\epsilon)(x) &= \lim_{i \rightarrow \infty} \int h(x) d\nu_{t_i}^\epsilon(x) - \int \int h(y) dP_x^\epsilon(y) d\nu_{t_i}^\epsilon(x) \\
&= \lim_{i \rightarrow \infty} \frac{1}{t_i} \sum_{t=1}^{t_i} \left( h(X_t^\epsilon) - \int h(y) dP_{X_t^\epsilon}^\epsilon(y) \right) \\
&= \lim_{i \rightarrow \infty} \frac{1}{t_i} \sum_{t=1}^{t_i} (h(X_t^\epsilon) - E[h(X_t^\epsilon) | \mathcal{F}_{t-1}]) \\
&\quad + \frac{1}{t_i} (E[h(X_1^\epsilon) | \mathcal{F}_0] - E[h(X_{t_i+1}^\epsilon) | \mathcal{F}_{t_i}]) \\
&= 0
\end{aligned}$$

with probability one. Since  $h$  is an arbitrary continuous bounded function and  $M$  is separable, the weak\* limit point  $\mu^\epsilon$  is with probability one an invariant Borel probability measure for  $X^\epsilon$ . ■

In particular this theorem with  $\epsilon = 0$  implies that if  $F$  has an attractor, then  $F$  has an invariant measure. The invariant measures for  $F$  may be quite numerous. For instance, any equilibrium or periodic orbit of  $F$ , whether stable or unstable, supports an invariant measure.

However, it is natural to assume that some of the invariant measures are more physically or biologically relevant than other invariant measures. For instance, intuition dictates that an invariant measure supported on an unstable fixed point is unlikely to be observed in nature, while an invariant measure supported on a stable fixed point is more likely to be observed. To pick out physically or biologically relevant invariant measures suppose that, for all  $\epsilon > 0$  sufficiently small,  $X^\epsilon$  has an invariant measure  $\mu^\epsilon$  as obtained in Theorem 1. A standard argument (see, e.g., Kifer [12]) implies that the weak\* limit points of these  $\mu^\epsilon$  as  $\epsilon \downarrow 0$  are  $F$ -invariant measures.

**Theorem 2.** *Let, for each  $\epsilon > 0$  sufficiently small,  $\mu^\epsilon$  be an invariant Borel probability measure for  $X^\epsilon$ . If  $\mu$  is a weak\* limit point of  $\mu^\epsilon$  as  $\epsilon \downarrow 0$ , then  $\mu$  is  $F$ -invariant.*

We define these weak\* limit points as *natural  $F$ -invariant measures*. An immediate corollary of Theorems 1 and 2 is the following.

**Corollary 1.** *If  $F$  admits an attractor, then  $F$  has a natural  $F$ -invariant measure.*

In the next two sections we investigate, under an additional set of assumptions, the supports of these natural invariant measures.

**4. Absorption preserving chain attractors.** To understand where the dynamics of  $X^\epsilon$  eventually settles when  $\epsilon > 0$  is small, we define in this section absorption preserving chain attractors. These attractors generalize the notion of attractor as introduced by Ruelle in [16], which are obtained for dynamical systems under arbitrarily small perturbations in case the absorbing  $\pi$ -system consists solely of a compact state space. Absorption preserving chain attractors also are a generalization of the extinction preserving chain attractors, defined in [10] for unstructured populations and extended in [7] to the case of structured populations. Extinction preserving chain attractors for a community-dynamical system under arbitrarily small perturbations are equal to absorption preserving chain attractors in case the absorbing  $\pi$ -system is taken to be the community state space together with the collection of all extinction sets for the populations. The derivation below is an adaptation of the derivation of extinction preserving chain attractors as presented in section 3 of [10] to discrete-time dynamical systems and absorbing  $\pi$ -systems. We take the state space  $M$  to be compact, e.g., by restricting ourselves to a compact global attractor.

**Definition 5.** *Let  $\epsilon \geq 0$ . A sequence  $x_0, \dots, x_n$  of elements in  $M$  such that  $d(x_{t+1}, F(x_t)) \leq \epsilon$  and  $x_{t+1} \in \mathcal{A}^*(F(x_t))$  for all  $t \in \{0, \dots, n-1\}$  is called an absorption preserving  $\epsilon$ -pseudo-orbit (or ap  $\epsilon$ -pseudo-orbit) of  $F$ .*

An ap  $\epsilon$ -pseudo-orbit  $x_0, \dots, x_n$  is said to have length  $n$  and to go from  $x_0$  to  $x_n$ . Two ap  $\epsilon$ -pseudo-orbits  $x_0, \dots, x_n$  and  $y_0, \dots, y_m$  of lengths  $n$  and  $m$ , respectively, and with  $d(y_0, F(x_n)) \leq \epsilon$  and  $y_0 \in \mathcal{A}^*(F(x_n))$  by concatenation can be combined into the ap  $\epsilon$ -pseudo-orbit  $x_0, \dots, x_n, y_0, \dots, y_m$  of length  $n + m + 1$  going from  $x_0$  to  $y_m$ . The notion of an absorption preserving  $\epsilon$ -pseudo-orbit reflects the character of irreversibility attached to absorption. In addition, we define *ap-chain recurrency* as follows.

**Definition 6.** *A point  $x$  is ap-chain recurrent if for every  $\epsilon > 0$  and every  $n > 0$  there is an ap  $\epsilon$ -pseudo-orbit of length  $\geq n$  going from  $x$  to  $x$ . The set of ap-chain recurrent points is called the ap-chain recurrent set.*

Using ap-pseudo-orbits, we introduce a partial ordering on  $M$  and a corresponding equivalence relation on  $M$ .

**Definition 7.** For  $x, y \in M$  we define  $x \succ_{ap} y$  (“ $x$  ap-chains to  $y$ ”) if for every  $\epsilon > 0$  there exists an ap  $\epsilon$ -pseudo-orbit going from  $x$  to  $y$ .

The relation  $\succ_{ap}$  (to be called *ap-chaining*) is a preorder on  $M$ . Ap-chaining is not necessarily a closed relation: if  $(x_i)_{i \geq 0}$  and  $(y_i)_{i \geq 0}$  are two sequences in  $M$  that converge to  $x$  and  $y$ , respectively, and are such that  $x_i \succ_{ap} y_i$  for all  $i$ , then not necessarily  $x \succ_{ap} y$ ; e.g., take  $x$  and  $y$  such that  $\mathcal{A}^*(x) \cap \mathcal{A}^*(y) = \emptyset$ .

**Definition 8.** For elements  $x, y \in M$ , define  $x \sim_{ap} y$  if  $x \succ_{ap} y$  and  $y \succ_{ap} x$ .

Since  $\succ_{ap}$  is a preorder,  $\sim_{ap}$  is an equivalence relation on  $M$ , to be called *mutual ap-chaining*. The equivalence class of  $x$  under  $\sim_{ap}$  is denoted as  $[x]_{ap}$ , and  $\mathcal{M}_{ap}$  denotes the set of equivalence classes in  $M$  under  $\sim_{ap}$ . The expression  $x \sim_{ap} y$  (“ $x$  and  $y$  ap-chain to each other”) implies that both  $x$  and  $y$  belong to  $\mathcal{A}^*(x) \cap \mathcal{A}^*(y)$ , and consequently  $\mathcal{A}^*(x) = \mathcal{A}^*(y)$ . In the sense indicated above, the relation  $\sim_{ap}$  may not be closed.

**Definition 9.**  $[x]_{ap}$  is called an ap-basic class if  $x$  is ap-chain recurrent.

Three equivalent statements can be made for ap-basic classes, as follows.

**Proposition 1.** The following three statements are equivalent:

1.  $[x]_{ap}$  is an ap-basic class;
2.  $x$  is a fixed point, or  $[x]_{ap}$  contains more than one point;
3. for all  $t \geq 0$ ,  $F^t([x]_{ap}) = [x]_{ap}$ .

**Definition 10.** For elements  $[x]_{ap}, [y]_{ap} \in \mathcal{M}_{ap}$  the relation  $\geq_{ap}$  is defined by  $[x]_{ap} \geq_{ap} [y]_{ap}$  if  $x \succ_{ap} y$ .

The relation  $\geq_{ap}$  (to be called *ap-connecting*) is a partial ordering on the set of equivalence classes of  $\sim_{ap}$ . By means of  $\geq_{ap}$  we define ap-chain attractors for dynamical systems with absorbing  $\pi$ -systems.

**Definition 11.**  $[x]_{ap}$  is an ap-chain attractor for  $(F, \mathcal{A})$  if it is a minimal element of the ordering  $\geq_{ap}$ .

An ap-chain attractor is an ap-basic class, and, by Proposition 1, contains the  $\omega$ -limit sets of all its elements. Existence of ap-chain attractors follows the same line of reasoning that guarantees the existence of attractors as presented by Ruelle in [16], which uses Zorn’s lemma and the fact that  $M$  is compact. In particular an ap-chain attractor will be closed.

**Definition 12.** For an ap-chain attractor  $[x]_{ap}$ , the collection of points  $\{y \in M : y \succ_{ap} x\}$  is called the basin of ap-chain attraction of  $[x]_{ap}$ .

The basin of ap-chain attraction for an ap-chain attractor  $[x]_{ap}$  is not empty, since  $x \in [x]_{ap}$ . Furthermore, each element in  $M$  belongs to the basin of ap-chain attraction of at least one ap-chain attractor.

**5. Random perturbations and ap-chain attractors.** In this section we assume that  $F : M \rightarrow M$  is dissipative. We show that when  $\epsilon > 0$  is sufficiently small,  $X^\epsilon$  spends most of its time near the ap-chain attractors of  $F$ . To accomplish this goal, we need to place the following two additional hypotheses on  $X^\epsilon$ :

- H2. For each  $\epsilon > 0$  there exists a  $\delta = \delta(\epsilon) \in (0, \epsilon)$  such that  $P_x^\epsilon(N_{ap}(y, \gamma)) > 0$  for all  $x, y \in M$  and  $\gamma > 0$  satisfying  $N_{ap}(y, \gamma) \subset N_{ap}(F(x), \delta)$ .
- H3. For each  $\epsilon > 0$ , if  $P_x^\epsilon(K) > 0$  for a closed set  $K \subset M$ , then there exists a neighborhood  $U$  (depending on  $x$  and  $\epsilon$ ) of  $x$  such that  $\inf_{y \in U} P_y^\epsilon(K) > 0$ .

H2 ensures that “the noise extends locally in all directions that respect the absorbing  $\pi$ -system.” H3 is a crude continuity-like condition on the supports of the random perturbations. Even in the case  $\mathcal{A} = \{M\}$ , these additional assumptions are weaker than those used by Ruelle [16] and Kifer [12]. The additional assumptions are immediately satisfied, for instance, for ecological or replicator equations with demographic stochasticity as described in sections 2.1 and 2.2. In the case of models  $X^\epsilon$  with  $k$  age classes and demographic stochasticity as described in section 2.3, these additional assumptions are satisfied by replacing the map  $F$  with  $F^k$ , and the states  $X_t^\epsilon$  with  $X_{kt}^\epsilon$ .

**Theorem 3.** *Let  $F : M \rightarrow M$  be dissipative,  $\mathcal{A}$  be an absorbing  $\pi$ -system for  $F$ , and  $X^\epsilon$  be a Markov chain which satisfies H1–H3. If  $x \in M$  does not lie in an ap-chain attractor for  $(F, \mathcal{A})$ , then there exists a neighborhood  $U$  of  $x$  such that*

$$(2) \quad P(X^\epsilon \text{ enters } U \text{ infinitely often}) = 0$$

whenever  $\epsilon > 0$  is sufficiently small.

In principle, the proof of the theorem adapts the proof of Kifer [12, Thm. 4.5] to the absorption preserving case. However, due to our formulation of H2 (i.e., the support of  $P_x^\epsilon$  includes  $N_{ap}(F(x), \delta)$  instead of including  $F(N_{ap}(x, \delta))$ ), our proof is shorter and more direct.

*Proof.* Assume that  $x \in M$  does not lie in an ap-chain attractor. We will show that there exist points  $y \in M$  and  $\epsilon > 0$  such that  $x$  ap-chains to  $y$  but there exists no ap  $\epsilon$ -pseudo-orbit from any element in  $N_{ap}(y, \epsilon)$  to any element in  $N_{ap}(x, \epsilon)$ . Since  $x$  does not lie in an ap-chain attractor, there exists a point  $y \in M$  such that  $x$  ap-chains to  $y$  but  $y$  does not ap-chain to  $x$ . Choose  $\epsilon > 0$  sufficiently small such that there exists no ap  $2\epsilon$ -pseudo-orbit from  $y$  to  $x$ . We proceed in two cases. First, suppose that  $\mathcal{A}^*(F(y)) = \mathcal{A}^*(y)$ . Then continuity implies that there exists  $\eta > 0$  such that  $F(N_{ap}(y, \eta)) \subset N_{ap}(F(y), \epsilon)$ . Since there are no ap  $2\epsilon$ -pseudo-orbits from  $F(y)$  to  $x$ , there are no ap  $\epsilon$ -pseudo-orbits from any element in  $N_{ap}(y, \eta)$  to any element in  $N_{ap}(x, \epsilon)$ . Replacing  $\epsilon$  with  $\min\{\eta, \epsilon\}$  completes this case. For the second case, suppose that  $\mathcal{A}^*(F(y)) \subsetneq \mathcal{A}^*(y)$ . Since  $x$  ap-chains to  $y$ , we have  $\mathcal{A}^*(y) \subseteq \mathcal{A}^*(x)$  and  $x \notin \mathcal{A}^*(F(y))$ . By H1, there is no ap  $\epsilon$ -pseudo-orbit from  $F(y)$  to  $x$ . Since  $x$  ap-chains to  $F(y)$ , replacing  $y$  with  $F(y)$  completes this case.

Let  $\delta = \delta(\epsilon) > 0$  be as given by H2. Let  $x_0 = x, x_1, \dots, x_n = y$  be an ap  $\delta$ -pseudo-orbit from  $x$  to  $y$ . H2 and H3 allow us to find a neighborhood  $U$  of  $x$ , an  $\alpha > 0$ , and a  $\gamma \in (0, \delta)$  such that

$$P_z^\epsilon(N_{ap}(x_1, \gamma)) \geq \alpha$$

for all  $z \in U$  and such that

$$P_z^\epsilon(N_{ap}(x_{i+1}, \gamma)) \geq \alpha$$

for all  $z \in N_{ap}(x_i, \gamma)$  and  $i = 1, \dots, n-1$ . Define  $U(0) = U$  and  $U(i) = N_{ap}(x_i, \gamma)$  for  $i = 1, \dots, n$ . We claim that

$$(3) \quad P(X_n^\epsilon \in U(n) | X_0^\epsilon = z) \geq \alpha^n \quad \text{for all } z \in U(0).$$

To prove (3) notice that

$$P(X_n^\epsilon \in U(n) | X_0^\epsilon = z) = \int \cdots \int P_{z_{n-1}}^\epsilon(U(n)) dP_{z_{n-2}}^\epsilon(z_{n-1}) \cdots dP_z^\epsilon(z_1).$$

Since  $P_z^\epsilon(U(n)) \geq \alpha 1_{U(n-1)}(z)$  for all  $z \in M$ , we get that

$$\begin{aligned} P(X_n^\epsilon \in U(n) | X_0^\epsilon = z) &\geq \alpha \int \cdots \int 1_{U(n-1)}(z_{n-1}) dP_{z_{n-2}}^\epsilon(z_{n-1}) \cdots dP_z^\epsilon(z_1) \\ &= \alpha \int \cdots \int P_{z_{n-2}}^\epsilon(U(n-1)) dP_{z_{n-3}}^\epsilon(z_{n-2}) \cdots dP_z^\epsilon(z_1). \end{aligned}$$

Similarly, applying the estimates  $P_z^\epsilon(U(n-i)) \geq \alpha 1_{U(n-i-1)}(z)$  for  $i = 1, \dots, n-1$  yields (3). The following standard result in Markov chain theory (see, e.g., [4, Chap. 5, Thm. 2.3]) applied to  $X = X^\epsilon$ ,  $B = U(n)$ , and  $C = U(0)$  yields that

$$P(X^\epsilon \text{ enters } U(0) \text{ infinitely often}) = 0.$$

**Theorem 4.** *Let  $X$  be a Markov chain, and suppose that*

$$P\left(\bigcup_{m=t+1}^{\infty} \{X_m \in B\} \mid X_t\right) \geq \beta > 0 \text{ on } \{X_t \in C\}.$$

Then

$$P(\{X \text{ enters } C \text{ infinitely often}\} \setminus \{X \text{ enters } B \text{ infinitely often}\}) = 0.$$

In the words of Chung [4, p. 256]: “The intuitive meaning of the preceding theorem has been given by Doeblin as follows: if the chance of a pedestrian’s getting run over is greater than  $\beta > 0$  each time he crosses a certain street, then he will not be crossing it indefinitely (since he will be killed first).” In our case “the certain street” is the set  $U(0)$  and “getting run over” is  $X^\epsilon$  following an ap  $\epsilon$ -pseudorbit from  $U(0)$  to  $U(n)$ . Any time that  $X^\epsilon$  enters  $U(n)$  it will never return to  $U(0)$ , as there are no ap  $\epsilon$ -pseudo-orbits back from  $U(n)$  to  $U(0)$ . ■

Recall from Theorem 1 that limit points  $\mu^\epsilon$  of the empirical measures  $\nu_t^\epsilon = \frac{1}{t} \sum_{i=1}^t \delta_{X_i^\epsilon}$  as  $t \rightarrow \infty$  are invariant measures for  $X^\epsilon$ . Moreover, by Theorem 2, limit points of these  $\mu^\epsilon$  as  $\epsilon \downarrow 0$  are natural invariant measures of  $F$ . Theorem 3 yields the following corollary, which implies that the natural  $F$ -invariant measures are concentrated on  $F$ ’s ap-chain attractors. Consequently,  $X^\epsilon$  spends most of its time near  $F$ ’s ap-chain attractors when  $\epsilon > 0$  is sufficiently small.

**Corollary 2.** *Let  $F : M \rightarrow M$  be dissipative, and let  $\mathcal{A}$  be an absorbing  $\pi$ -system for  $F$ . Let  $\{X^\epsilon, \epsilon > 0\}$  be a collection of Markov chains that satisfy H1–H3, and let  $\mu^\epsilon$  denote an invariant Borel probability measure for  $X^\epsilon$ . All weak\* limit points of  $\mu^\epsilon$  as  $\epsilon \downarrow 0$  are supported by the ap-chain attractors for  $(F, \mathcal{A})$ .*

*Proof.* For all  $\epsilon > 0$ , let  $\mu^\epsilon$  be an invariant Borel probability measure for  $X^\epsilon$ . Let  $x \in M$  not lie in any ap-chain attractor. Then there exists an open neighborhood  $U$  of  $x$  such that

$$\mu^\epsilon(U) = 0$$

for  $\epsilon > 0$  sufficiently small. Since  $U$  is an open set,  $\mu(U) = 0$  for any weak\* limit point  $\mu$  of  $\mu^\epsilon$  as  $\epsilon \downarrow 0$ . Since  $x$  was an arbitrary point in the complement of the ap-chain attractors, it follows that  $\mu$  is supported by the ap-chain attractors. ■

Often, attractors for  $F$  break up into a finite number of ap-chain attractors for  $(F, \mathcal{A})$ . When this occurs, the following result shows that for sufficiently small  $\epsilon > 0$ ,  $X^\epsilon$  eventually remains in an ap  $\epsilon$ -neighborhood of one of these ap-chain attractors. Moreover, for  $\epsilon > 0$  sufficiently small,  $X^\epsilon$  reaches an ap-chain attractor with positive probability only if  $X_0^\epsilon$  ap-chains to an ap-chain attractor.

**Theorem 5.** *Let  $F : M \rightarrow M$  be dissipative,  $\mathcal{A}$  be an absorbing  $\pi$ -system for  $F$ ,  $\{X^\epsilon, \epsilon > 0\}$  be a collection of Markov chains that satisfy H1–H3, and  $X_0^\epsilon = x_0 \in M$  for all  $\epsilon > 0$ . Assume that there exist  $k$  compact subsets  $K_1, \dots, K_k$  of  $M$  such that*

- for each  $K_i$  there exists an  $A \in \mathcal{A}$  such that  $K_i \subset A$  and  $K_i$  is an attractor for  $F|_A$ ;
- $\cup_i K_i$  contains all the ap-chain attractors for  $(F, \mathcal{A})$ .

Then for any  $\gamma > 0$  and  $\epsilon > 0$  sufficiently small

$$(4) \quad P(\text{there exist } s \text{ and } i \text{ such that for all } t \geq s : X_t^\epsilon \in N_{ap}(K_i, \gamma)) = 1.$$

Moreover, if  $x_0$  ap-chains to a point in  $K_i$ , then for any  $\gamma > 0$  and  $\epsilon > 0$  sufficiently small

$$(5) \quad P(\text{there exists an } s \text{ such that for all } t \geq s : X_t^\epsilon \in N_{ap}(K_i, \gamma)) > 0.$$

If  $x_0$  does not ap-chain to any point in  $K_i$ , then there is a  $\gamma > 0$  such that

$$(6) \quad P(\text{there exists an } s \text{ such that for all } t \geq s : X_t^\epsilon \in N_{ap}(K_i, \gamma)) = 0$$

whenever  $\epsilon > 0$  is sufficiently small.

*Proof.* The proof of the theorem relies on the following two lemmas.

**Lemma 1.** *Let  $F : M \rightarrow M$  be a dissipative map and  $\mathcal{A}$  be an absorbing  $\pi$ -system for  $F$ . For  $A \in \mathcal{A}$ , let  $B$  be an attractor for  $F|_A$ . Then for every  $\gamma > 0$  there exist  $\epsilon_0 > 0$  and  $\beta \in (0, \gamma)$  such that there is no ap  $\epsilon_0$ -pseudo-orbit from  $x$  to  $y$  for all  $x \in N_{ap}(B, \beta)$  and  $y \in M \setminus N_{ap}(B, \gamma)$ .*

*Proof.* Suppose that the conclusion of the proposition does not hold. Then there is a  $\gamma > 0$  for which there do not exist an  $\epsilon_0 > 0$  and  $\beta \in (0, \gamma)$  such that there is no ap  $\epsilon_0$ -pseudo-orbit from  $x$  to  $y$  for all  $x \in N_{ap}(B, \beta)$  and  $y \in M \setminus N_{ap}(B, \gamma)$ . I.e., in that case, for every  $\epsilon_0 > 0$  and every  $\beta \in (0, \gamma)$  there is an ap  $\epsilon_0$ -pseudo-orbit from an  $x \in N_{ap}(B, \beta)$  to a  $y \in M \setminus N_{ap}(B, \gamma)$ . Consequently, by letting  $\epsilon_0$  and  $\beta$  become infinitesimally small (but positive), it follows that there exists an  $x \in B$  that ap-chains to an element  $y \in M \setminus N_{ap}(B, \gamma)$ . Necessarily, any compact neighborhood  $U$  of  $B$  in  $A$  contains part of the set  $\{z \in M : x \succ_{ap} z\}$  by which  $x$  ap-chains to  $y$ , and therefore  $\omega(U) \supseteq B$ . This contradicts that  $B$  is an attractor for  $F|_A$ . ■

**Lemma 2.** *Let  $F : M \rightarrow M$  be dissipative with global attractor  $B$ ,  $\mathcal{A}$  be an absorbing  $\pi$ -system for  $F$ ,  $\{X^\epsilon, \epsilon > 0\}$  be a collection of Markov chains that satisfy H1, and  $S \subset M$  be a compact set such that  $\text{supp}(\{X_0^\epsilon\}) = S$  for all  $\epsilon > 0$ . Then for every  $\gamma > 0$  there exist an  $\epsilon_1 > 0$  and  $n \geq 0$  such that for all  $\epsilon \in (0, \epsilon_1]$*

$$P(\text{for all } t \geq n : X_t^\epsilon \in N(B, \gamma)) = 1.$$

*Proof.* It suffices to prove the lemma for the case in which  $\mathcal{A} = \{M\}$ . Since  $F$  is dissipative, there exists a compact attractor  $B$  whose basin of attraction is  $M$ . Let  $S$  be as in the lemma. Let  $\gamma > 0$  be given, and for this  $\gamma$  choose  $\epsilon_0 > 0$ ,  $\beta \in (0, \gamma)$  as given by Lemma 1. Lemma 1 implies that there does not exist an ap  $\epsilon_0$ -pseudo-orbit from  $N_{ap}(B, \beta)$  to  $M \setminus N_{ap}(B, \gamma)$ . Since  $S$  is compact and lies in the basin of attraction of  $B$ , there exists an  $n$  such that  $F^n(S) \subset N(B, \beta/2)$ . Compactness of  $S$  and continuity of  $F$  imply that there exists an  $\epsilon_1 \in (0, \min\{\epsilon_0, \frac{\beta}{2}\})$  such that every ap  $\epsilon_1$ -pseudo-orbit  $x_0, \dots, x_n$  with  $x_0 \in S$  satisfies  $x_n \in N(B, \beta)$ . For any Markov chain  $X^\epsilon$  that satisfies H1 it follows that if  $\epsilon \leq \epsilon_1$ , then for any  $t \geq 0$  the sequence  $X_0^\epsilon, \dots, X_t^\epsilon$  is an ap  $\epsilon_1$ -pseudo-orbit. Since  $X_0^\epsilon \in S$ , we get with probability one that  $X_n^\epsilon \in N(B, \beta)$  and  $X_t^\epsilon \in N(B, \gamma)$  for  $t \geq n$  whenever  $\epsilon \in (0, \epsilon_1]$ . ■

Let  $B$  be the global attractor of  $F$ , and let  $\gamma > 0$  be given. Lemma 2 implies that there exist an  $\epsilon_0 > 0$  and  $n \geq 0$  such that  $P(\text{for all } t \geq n : X_t^\epsilon \in K) = 1$  whenever  $\epsilon \in (0, \epsilon_0]$ . Applying Lemma 1 to each of the  $K_i$  implies that there exist  $\epsilon_1 \in (0, \epsilon_0)$  and  $\beta_1 \in (0, \gamma)$  such that for all  $1 \leq i \leq k$  there is no ap  $\epsilon_1$ -pseudo-orbit from any point in  $N_{ap}(K_i, \beta_1)$  to any point in  $M \setminus N_{ap}(K_i, \gamma)$ . Next, we wish to extend the “absorption preserving” neighborhoods  $N_{ap}(K_i, \beta_1)$  of each of the  $K_i$ ’s to full neighborhoods of the  $K_i$ ’s such that  $X^\epsilon$  cannot enter them too often without getting stuck. Let  $\delta(\epsilon)$  be as given by H2. Since  $K_i$  is  $F$ -invariant, for every  $\epsilon > 0$  there exists  $\eta = \eta(\epsilon) \in (0, \beta_1)$  such that  $F(x) \in N(K_i, \delta(\epsilon)/2)$  whenever  $x \in N(K_i, \eta)$ . H1–H3 imply that  $\inf_{x \in N(K_i, \eta)} P_x^\epsilon(A_i) > 0$ . Applying Theorem 4 with  $C = N(K_i, \eta) \setminus A_i$  and  $B = A_i$  implies that for all  $\epsilon > 0$  and each  $1 \leq i \leq k$

$$(7) \quad P(X_t^\epsilon \in N(K_i, \eta) \setminus A_i \text{ infinitely often}) = 0.$$

Let  $\text{int}(N(K_i, \eta))$  denote the interior of  $N(K_i, \eta)$ . Since  $\eta$  is strictly positive, every  $x \in K \setminus \bigcup_{i=1}^k \text{int}(N(K_i, \eta))$  does not lie in an ap-chain attractor. Theorem 3 implies that for every  $x \in K \setminus \bigcup_{i=1}^k \text{int}(N(K_i, \eta))$  there exists a neighborhood  $U_x$  of  $x$  and  $\epsilon_x > 0$  such that for all  $\epsilon \in (0, \epsilon_x)$ :  $P(X_t^\epsilon \in U_x \text{ infinitely often}) = 0$ . Compactness of  $K \setminus \bigcup_{i=1}^k \text{int}(N(K_i, \eta))$  implies that  $K \setminus \bigcup_{i=1}^k \text{int}(N(K_i, \eta))$  is covered by a finite number of these open neighborhoods, say  $U_{x_1}, \dots, U_{x_n}$ . Let  $\epsilon_2 = \min\{\epsilon_{x_1}, \dots, \epsilon_{x_n}, \epsilon_1\}$ . Since  $X^\epsilon$  can enter each element of this finite collection of neighborhoods only finitely often,

$$(8) \quad P\left(X_t^\epsilon \in K \setminus \bigcup_{i=1}^k \text{int}(N(K_i, \eta)) \text{ infinitely often}\right) = 0$$

for all  $\epsilon \in (0, \epsilon_2)$ .

Equations (7) and (8) imply that

$$P\left(X_t^\epsilon \in K \setminus \bigcup_{i=1}^k N_{ap}(K_i, \eta) \text{ infinitely often}\right) = 0$$

for all  $\epsilon \in (0, \epsilon_2)$ . Our choice of  $K$  implies that

$$P\left(X_t^\epsilon \in M \setminus \bigcup_{i=1}^k N_{ap}(K_i, \eta) \text{ infinitely often}\right) = 0$$

for all  $\epsilon \in (0, \epsilon_2)$ . It follows that

$$P\left(X_t^\epsilon \in \bigcup_{i=1}^k N_{ap}(K_i, \eta) \text{ for some } t \geq 0\right) = 1$$

for all  $\epsilon \in (0, \epsilon_2)$ . Since there are no  $\epsilon_2$ -pseudo-orbits from  $N_{ap}(K_i, \eta)$  to  $M \setminus N_{ap}(K_i, \eta)$  for  $i = 1, \dots, k$ , expression (4) follows.

To prove (5), assume that  $x_0$  does ap-chain to  $y \in K_i$ . Then the arguments leading to (3) imply that  $P(X_t^\epsilon \text{ enters } N_{ap}(K_i, \eta) \text{ for some } t) > 0$ . Since there are no ap  $\epsilon_2$ -pseudo-orbits from  $N_{ap}(K_i, \eta)$  to  $M \setminus N_{ap}(K_i, \eta)$ , expression (5) follows.

To prove (6), assume that  $x_0$  does not ap-chain to any point in  $K_i$ . For every point  $y \in K_i$ , there exists an  $\epsilon_y > 0$  such that there are no ap  $2\epsilon_y$ -pseudo-orbits from  $x_0$  to  $y$ . Hence, there are no ap  $\epsilon_y$ -pseudo-orbits from  $x_0$  to any point in  $N_{ap}(y, \epsilon_y)$ . Since  $K_i$  is compact, there are  $y_1, \dots, y_n$  such that  $K_i \subset \cup_j N_{ap}(y_j, \epsilon_{y_j})$ . Let  $\epsilon_3 = \min_j \{\epsilon_{y_j}\}$ . Then there are no ap  $\frac{\epsilon_3}{2}$ -pseudo-orbits from  $x_0$  to any point in  $N_{ap}(K_i, \frac{\epsilon_3}{2})$ . Hence (6) holds for  $0 < \epsilon < \frac{\epsilon_3}{2}$  and  $\gamma > 0$  sufficiently small. ■

**6. Applications.** In this section, we apply the results from the previous sections to models of competing species and replicator dynamics.

**6.1. Ecological drift for competing species.** When the ecological outcome of competing species is determined by stochastic forces, ecological drift is said to occur. Here we illustrate two scenarios, ecologically equivalent competing species and intermingled basins of competitive exclusion, for which ecological drift occurs. Let  $x_1$  and  $x_2$  be the densities of two competing species. The competing species are ecologically equivalent if the per capita growth of each species is of the form  $f(x_1 + x_2)$ , in which case the competitive dynamics are given by  $F(x_1, x_2) = (x_1 f(x_1 + x_2), x_2 f(x_1 + x_2))$ . The following proposition proves that, under suitable assumptions on  $f$  and the noise, ecological drift occurs in the sense that competitive exclusion of either species occurs with positive probability for all positive initial conditions. Figure 1 illustrates how the probability of exclusion can depend on initial conditions for the map  $F(x_1, x_2) = (3.9x_1(1 - x_1 - x_2), 3.9x_2(1 - x_1 - x_2))$  with additive uniformly distributed noise on  $[-0.01, 0.01]$ .

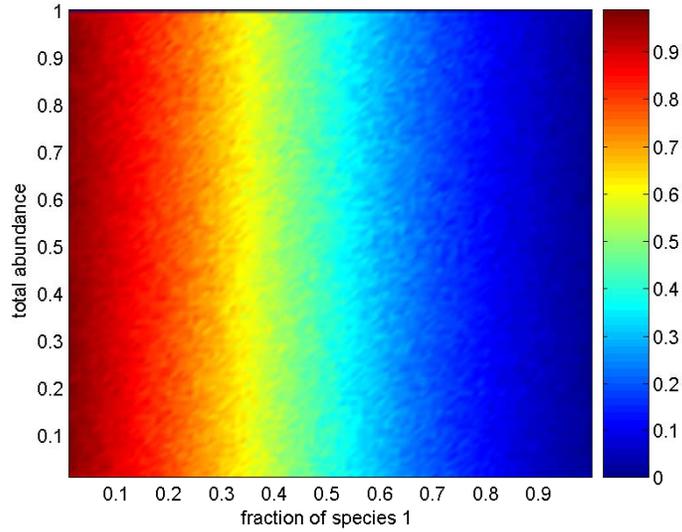
**Proposition 2.** *Let  $m > 0$  (i.e., the maximum density supported by the population) and  $M = \{(x_1, x_2) \in \mathbf{R}_+^2 : x_1 + x_2 \leq m\}$ . Let  $f : [0, m] \rightarrow \mathbf{R}_+$  be a continuous decreasing function with  $f(0) > 1$ ,  $f(m) < 1$ ,  $f > 0$  on  $[0, m)$ , and  $xf(x) \leq m$  for all  $x \in [0, m]$ . Let  $F(x_1, x_2) = (x_1 f(x_1 + x_2), x_2 f(x_1 + x_2))$ ,  $\mathcal{A} = \{M, \{0\} \times [0, m], [0, m] \times \{0\}, (0, 0)\}$ , and  $\{X^\epsilon, \epsilon > 0\}$  be a collection of Markov chains satisfying H1–H3. Then there exists a  $\delta > 0$  such that for all  $x_1 x_2 > 0$  and  $\epsilon > 0$  sufficiently small*

$$P_x^\epsilon(X_t^\epsilon \in \{0\} \times [a, m] \cup [a, m] \times \{0\} \text{ for } t \text{ sufficiently large}) = 1,$$

$$P_x^\epsilon(X_t^\epsilon \in \{0\} \times [a, m] \text{ for } t \text{ sufficiently large}) > 0,$$

and

$$P_x^\epsilon(X_t^\epsilon \in [a, m] \times \{0\} \text{ for } t \text{ sufficiently large}) > 0.$$

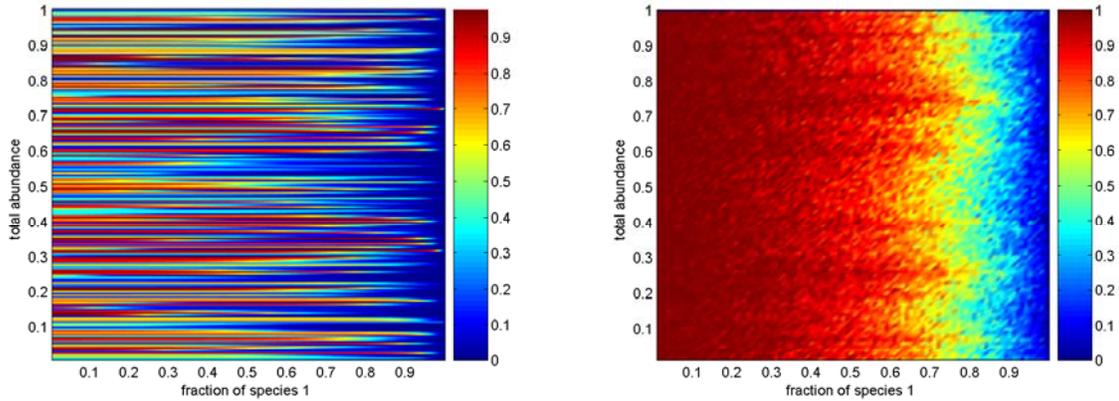


**Figure 1.** The probability of extinction of species 1 as a function of the initial conditions. These probabilities were computed for the map  $F(x_1, x_2) = (3.9x_1(1-x_1-x_2), 3.9x_2(1-x_1-x_2))$  with additive uniformly distributed noise on  $[-0.01, 0.01]$ .

*Proof.* Consider the change of variables  $u = x_1 + x_2$  and  $v = \frac{x_2}{x_1+x_2}$ . In this coordinate system,  $F$  is given by  $G(u, v) = (uf(u), v)$ , provided that  $u > 0$ , and  $M$  is given by  $[0, m] \times [0, 1]$ . Our assumptions of  $f$  imply that there is an attractor  $A_1 \subset (0, m)$  for  $u \mapsto uf(u)$  whose basin of attraction is  $(0, m)$ . Hence,  $A = A_1 \times [0, 1]$  is an attractor for  $G$  with a basin of attraction including  $(0, m) \times [0, 1]$ . The basin of attraction does not include  $\{m\} \times [0, 1]$  whenever  $f(m) = 0$ . Since  $G_2(u, v) = v$ , all points in  $(0, m) \times [0, 1]$  ap-chain to points in  $A_1 \times \{0\}$  and to points in  $A_1 \times \{1\}$ . Applying Theorem 5 completes the proof of the proposition. ■

Another way that ecological drift can occur is when the competing species exhibit *intermingled basins of competitive exclusion*. In the words of [8], this occurs when for “almost all initial conditions one of the two species dies out. But the survivor is unpredictable: The basins of the two chaotic one species attractors are everywhere dense.” Hofbauer et al. [8] have proven the existence of an intermingled basin for a class of maps. For systems of this type, Theorem 5 implies the following proposition about ecological drift. Figure 2 illustrates a potential intermingled basin of competitive exclusion for  $F(x_1, x_2) = (3.9x_1(1-x_1-x_2)(1+0.1x_2 \sin(2\pi(x_1+x_2)))/(x_1+x_2)), 3.9x_2(1-x_1-x_2)(1-0.1x_1 \sin(2\pi(x_1+x_2)))/(x_1+x_2))$  and the effect of additive uniformly distributed noise.

**Proposition 3.** Let  $m > 0$  (i.e., the maximum density supported by the population) and  $M = \{(x_1, x_2) \in \mathbf{R}_+^2 : x_1 + x_2 \leq m\}$ ,  $F : M \rightarrow M$  be a continuous map of the form  $F(x_1, x_2) = (x_1 f_1(x_1, x_2), x_2 f_2(x_1, x_2))$ ,  $\mathcal{A} = \{M, \{0\} \times [0, m], [0, m] \times \{0\}, (0, 0)\}$ , and  $\{X^\epsilon, \epsilon > 0\}$  be a collection of Markov chains satisfying H1–H3. Assume that  $F$  has ap-chain attractors  $A_1 \subset (0, m) \times \{0\}$  and  $A_2 \subset \{0\} \times (0, m)$  such that each basin of attraction of  $A_i$  is dense in  $M$ ,  $A_1$ 's basin includes  $(0, m) \times \{0\}$ , and  $A_2$ 's basin includes  $\{0\} \times (0, m)$ . Then



**Figure 2.** Intermingled basins of competitive exclusion and the probability of extinction of species 2 as a function of the initial conditions. In the left panel, each initial condition for  $F(x_1, x_2) = (3.9x_1(1-x_1-x_2)(1+0.1x_2 \sin(2\pi(x_1+x_2)))/(x_1+x_2)), 3.9x_2(1-x_1-x_2)(1-0.1x_1 \sin(2\pi(x_1+x_2)))/(x_1+x_2))$  was iterated 1,000 time steps, and the final density of species 2 is plotted. Warmer colors correspond to higher densities, and cooler colors correspond to lower densities. In the right panel, the map was perturbed by additive uniformly distributed noise on  $[-0.01, 0.01]$ , and the probability of extinction of species 1 was computed for a grid of initial conditions.

there exists  $a > 0$  such that for all  $x_1 x_2 > 0$  and  $\epsilon > 0$  sufficiently small

$$P_x^\epsilon(X_t^\epsilon \in \{0\} \times [a, m] \cup [a, m] \times \{0\} \text{ for } t \text{ sufficiently large}) = 1,$$

$$P_x^\epsilon(X_t^\epsilon \in \{0\} \times [a, m] \text{ for } t \text{ sufficiently large}) > 0,$$

and

$$P_x^\epsilon(X_t^\epsilon \in [a, m] \times \{0\} \text{ for } t \text{ sufficiently large}) > 0.$$

**6.2. Asymmetric games.** In evolution, players in different positions may engage in asymmetric conflicts. For the case of two types of players and two strategies, one can assume without loss of generality that the payoff matrix for one type of player, say females, is of the form

$$\begin{bmatrix} 0 & a_{12} \\ a_{21} & 0 \end{bmatrix},$$

while the payoff matrix for the other type of player, say males, is of the form

$$\begin{bmatrix} 0 & b_{12} \\ b_{21} & 0 \end{bmatrix}.$$

For this payoff structure, the game dynamics is given by

$$(9) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x)(a_{12} - (a_{12} + a_{21})y), \\ \frac{dy}{dt} &= y(1-y)(b_{12} - (b_{12} + b_{21})x), \end{aligned}$$

where  $x$  and  $y$  are frequencies of strategy 1 for males and females, respectively. Let  $M = [0, 1] \times [0, 1]$ , let  $(\phi_t)_{t \geq 0}$  denote the flow of the game dynamics, and let  $F = \phi_h$  for some  $h > 0$ . The dynamics of this game is well studied (see Hofbauer and Sigmund [9]) and fall generically into the following four cases:

- I.  $a_{12}a_{21} < 0$ : One of the two strategies of the females dominates the other:  $x$  converges monotonically to 0 or 1.
- II.  $b_{12}b_{21} < 0$ : One of the two strategies of the males dominates the other:  $y$  monotonically converges to 0 or 1.
- III.  $a_{12}a_{21} > 0$ ,  $b_{12}b_{21} > 0$ , and  $a_{12}b_{12} > 0$ : There is a unique interior equilibrium

$$(x^*, y^*) = \left( \frac{b_{12}}{b_{12} + b_{21}}, \frac{a_{12}}{a_{12} + a_{21}} \right),$$

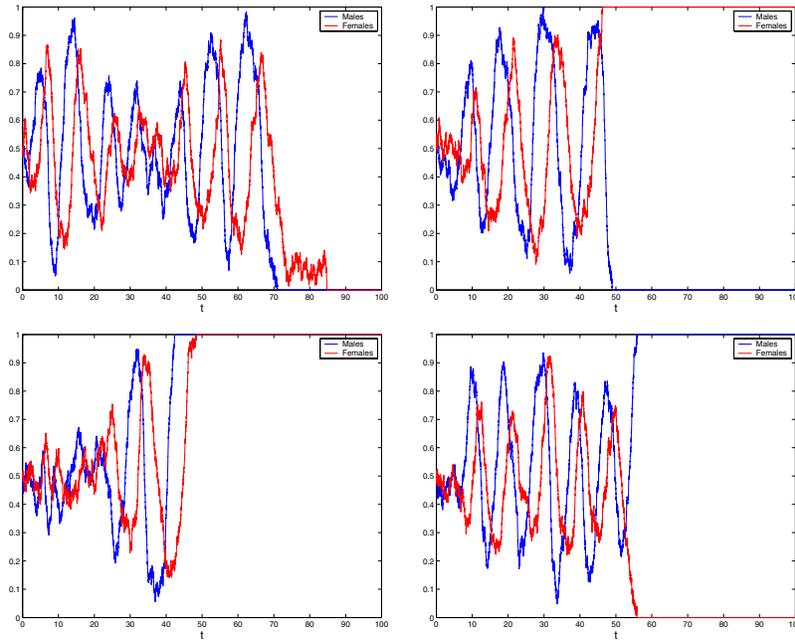
which is a saddle, and almost every initial condition converges to opposite corners of  $M$ .

- IV.  $a_{12}a_{21} > 0$ ,  $b_{12}b_{21} > 0$ , and  $a_{12}b_{12} < 0$ : The unique equilibrium  $(x^*, y^*)$  is neutrally stable, and all orbits in  $M$  are periodic orbits surrounding  $(x^*, y^*)$ .

Consider random perturbations  $X^\epsilon$  of  $F$  corresponding to demographic stochasticity with or without environmental stochasticity.  $X^\epsilon$  satisfies **H1–H3** with respect to the absorbing  $\pi$ -system generated by  $M$ ,  $\{(0, y) : y \in [0, 1]\}$ ,  $\{(1, y) : y \in [0, 1]\}$ ,  $\{(x, 0) : x \in [0, 1]\}$ , and  $\{(x, 1) : x \in [0, 1]\}$ . For cases **I–IV**, the only ap-chain attractors are the boundary equilibria  $(0, 1)$ ,  $(1, 0)$ ,  $(0, 0)$ , and  $(1, 1)$ . Hence, Theorem 5 implies that, with probability 1,  $X^\epsilon$  converges to one of these boundary equilibria in finite time. Moreover, if  $X_0^\epsilon \in (0, 1) \times (0, 1)$ , then for cases **I–III**,  $X^\epsilon$  converges with positive probability only to a subset of the boundary equilibria, while for case **IV**,  $X^\epsilon$  converges to any boundary equilibrium with positive probability (Figure 3).

**7. Discussion.** Our analysis studies the effect of localized noise on discrete-time dynamical systems with absorbing sets. Noise is represented by a discrete time Markov chain that in each time step acts on the deterministic image of a state. Certain regions of the state space are assumed to be absorbing, in that the system cannot leave (either deterministically or by a random perturbation) these regions once it has entered such a region, e.g., extinction boundaries in the absence of immigration or mutations. Thus, we assume that noise respects the absorbing sets (**H1**). We prove that if an unperturbed system has an attractor, then for sufficiently small perturbations the perturbed system has invariant probability measures that describe the asymptotic behavior of the system. Letting the size of the random perturbations go to zero, natural invariant measures for the unperturbed system are obtained as limit points of the invariant measures for the perturbed system. Provided that the random perturbations are sufficiently small, the asymptotic dynamics of the perturbed system is well described by these natural invariant measures.

Adding two more assumptions to our formalism—namely, within each absorbing set noise may locally perturb the dynamics into all admissible directions (**H2**), and nonzero noise is locally sustained (**H3**)—allows us to derive that the natural invariant measures of an unperturbed system are supported by the ap-chain attractors. First we show that if a state does not belong to an ap-chain attractor, then under sufficiently small perturbations, this state has a neighborhood which the system cannot enter infinitely often. Next we prove that, given



**Figure 3.** Four realizations of (9) are shown with  $a_{12} = a_{21} = 2$  and  $b_{12} = b_{21} = -2$  with demographic stochasticity of size  $\epsilon = 0.01$ .

that the ap-chain attractors are contained in the attractors of the unperturbed system, there exists an attractor such that for any neighborhood of that attractor and sufficiently small perturbations, the perturbed system will be restricted to that neighborhood within a finite amount of time. In addition, if small noise is capable of bringing a system into an attractor, then there is a positive probability that the randomly perturbed system will be restricted to an arbitrary neighborhood of that attractor within a finite amount of time.

Although our statements may sound intuitively clear, to our knowledge so far no mathematical proofs have been presented in the literature that support them, given our assumptions H1–H3 on the random perturbations. The papers [10] and [7] introduce the notion of extinction preserving chain attractors, but their relation to the effect of small random perturbations on the dynamics is dealt with only on the intuitive level and does not provide an analysis for the case of random perturbations. Ruelle in his paper [16] derives a result similar to ours if the full state space is the only absorbing set; namely, the randomly perturbed system statistically spends most of its time in a neighborhood of the chain attractors. However, even when the full state space is the only absorbing set, his work differs from ours in that our assumptions on the random perturbations are weaker [16, p. 145]. Moreover, our assumptions H2 and H3 on supports make the proof of our Theorem 3 and its Corollary 2 more straightforward than the proof of the similar statements in Ruelle’s setting, as follows from comparison of our proof with, e.g., a proof given by Kifer (the proof of Theorem 4.5 in [12]).

Since small random perturbations are omnipresent in reality, our work explains their effects on community dynamics. A combination of small random perturbations with larger perturbations might lead to a better understanding of fluctuations of population densities due

to the presence of multiple ap-chain attractors. Although sufficiently small perturbations, e.g., those due to environmental stochasticity, are likely to bring the system close to a specific ap-chain attractor, irregular appearances of sufficiently large perturbations might cause the system to change its basin of ap-chain attraction. Large random perturbations are not, however, covered by our framework, and their inclusion in the theory is a possible direction for further research.

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