

# On the Role of Spatial Aggregation in the Extinction of a Species

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**Abstract.** We compare two spatial stochastic models. The first, introduced by Schinazi (2005), shows that spatial aggregation may cause the extinction of a species in catastrophic times. The second shows that, for a certain range of parameters, spatial aggregation may help the survival of a species in non catastrophic times.

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## 1. Spatial aggregation may be bad in catastrophic times

There have been many documented mass extinctions of all sorts of animals in the last 60,000 years, see Martin and Klein (1984). In some cases the extinctions have occurred at a point in time suspiciously close to the arrival time of a new group of humans. One mass extinction theory is that human hunters waged a blitzkrieg against some species, quickly exterminating millions of animals. One such example is the extermination of Moa birds in New Zealand, see Diamond (2000) and Holdaway and Jacomb (2000). It seems that in a matter of a few decades, after the first settlements of Polynesians, all of the estimated 160,000 large flightless Moas disappeared. How could a few dozens of hunters provoke such a disaster? One hypothesis is that these animals were not afraid of humans and were therefore very easy to kill. Schinazi (2005) proposed a new hypothesis. In addition to their naive behavior these animals may have lived in very large flocks and once the flock was found by hunters it could be easily killed off. This could also explain how the Moas could be exterminated in one of the world's most rugged lands. Our hypothesis might be difficult to test on Moas. But there are documented examples of extinctions of animals living in huge flocks almost up to the end of

their species, for instance passenger pigeons (see Austin (1983)) or the American bison.

Schinazi (2005) proposed a mathematical model that, at least in theory, shows that animals living in large flocks are more susceptible to mass extinctions than animals living in small flocks. More precisely, if the maximum flock size is above a certain threshold then the population is certain to get extinct while if the maximum flock size is below the threshold there is a strictly positive probability that the population will survive.

The model is spatial and stochastic on the lattice  $\mathbb{Z}^d$ , typically  $d = 2$ . Each site of the lattice may host a flock of up to  $N$  individuals. Each individual may give birth to a new individual at the same site at rate  $\phi$  until the maximum of  $N$  individuals has been reached at the site. Once the flock reaches  $N$  individuals then, and only then, it starts giving birth on each of the  $2d$  neighboring sites at rate  $\lambda$ . This rule is supposed to mimic the fact that individuals like to stay in a flock and will give birth outside the flock only when the flock attains the maximum number  $N$  that a site may support. Finally, disaster strikes at rate 1, that is, the whole flock disappears. This rule mimics an encounter with greedy hunters or a new disease. Both disasters seem to have stricken the American buffalo and the passenger pigeon.

We now write the above description mathematically. Each site  $x$  of  $\mathbb{Z}^d$  may be in one of the states:  $0, 1, 2, \dots, N$  and this state is the size of the flock at  $x$ . The model is a continuous time Markov process that we denote by  $\eta_t$ . Let  $n_N(x, \eta_t)$  be the number of neighbors of site  $x$ , among its  $2d$  nearest neighbors, that are in state  $N$  at time  $t$ .

Assume that the model is in configuration  $\eta$ , then the state at a given site  $x$  evolves as follows:

$$\begin{aligned} i &\rightarrow i + 1 \text{ at rate } i\phi + \lambda n_N(x, \eta) \text{ for } 0 \leq i \leq N - 1 \\ i &\rightarrow 0 \text{ at rate } 1 \text{ for } 1 \leq i \leq N \end{aligned}$$

We will have two models in this paper. We call the model above Model I. We now explain the transition rules in words. Assume that a site  $x$  at a given time has  $j$  neighbors in state  $N$ ,  $j = 0, 1, 2, 3$  or  $4$  in  $d = 2$ . Then, if site  $x$  is in state  $i \leq N - 1$  there are two possibilities. Either, after an exponential random time  $T$  with rate  $a = i\phi + j\lambda$  (i.e.,  $P(T > t) = \exp(-at)$ ), site  $x$  goes to state  $i + 1$  or after an exponential random time with rate 1 site  $x$  goes to state 0. The first of the two random times that occur determines the outcome. If site  $x$  is in state  $N$  then it may give birth to an individual on a neighboring site (provided the neighboring site is not full) with rate  $\lambda$  or it may go to state 0 with rate 1.

In the special case where there is a maximum of one individual per site (i.e.,  $N = 1$ ) this model is well known and is called the contact process (see Liggett (1999)). For the contact process, there exists a critical value  $\lambda_c$  (that depends on the dimension  $d$  of the lattice) such that the population dies out if and only if  $\lambda \leq \lambda_c$ .

**Theorem 1.** *Assume that  $\lambda > \lambda_c$  (the critical value of the contact process) and that  $\phi > 0$ . Then, there is a critical positive integer  $N_c$ , depending on  $\lambda$  and  $\phi$ , such that for Model I on  $\mathbb{Z}^d$ , for any  $d \geq 1$ , the population dies out for  $N > N_c$  and survives for  $N < N_c$ .*

Theorem 1 is a particular case of a result proved in Schinazi (2005), see Corollary 2 there.

## 2. Aggregation may be good in non catastrophic times

We now consider a model with the same rules for births (in particular a flock may give birth outside its site only when it has  $N$  individuals) but with a different rule for deaths: they now occur one by one. We call the following Model II.

$$\begin{aligned} i &\rightarrow i + 1 \text{ at rate } i\phi + \lambda n_N(x, \eta) \text{ for } 0 \leq i \leq N - 1 \\ i &\rightarrow i - 1 \text{ at rate } i \text{ for } 1 \leq i \leq N \end{aligned}$$

This models the population in the absence of greedy hunters. As the reader will see below the role of  $N$  is strikingly different in Models I and II.

**Theorem 2.** *Consider Model II on  $\mathbb{Z}^d$  for a dimension  $d \geq 2$ . Assume that  $\lambda > 0$  and  $\phi > 1$ . There is a critical value  $N_c(\lambda, \phi)$  depending on  $\lambda$  and  $\phi$  such that if  $N > N_c$  then, starting from any finite number of individuals, the population has a strictly positive probability of surviving.*

Theorem 2 tells us that survival is possible for any internal birth rate  $\phi > 1$  and any external birth rate  $\lambda > 0$  provided  $N$  is large enough. On the other hand, if  $N = 1$  and  $\lambda < \lambda_c$  then the species dies out. Hence, for some parameters spatial aggregation makes the species survive. This is consistent with the so-called Allee effect in Ecology. See, for instance, Stephens and Sutherland (1999).

We believe Theorem 2 holds in  $d = 1$  as well but our (elementary) proof requires  $d \geq 2$ . This is so because we compare our stochastic model to a percolation model on  $\mathbb{Z}^d$  for which there is percolation only for  $d \geq 2$ . In order to prove Theorem 2 in  $d = 1$  we would need to use time as an extra dimension. This has been done many times since Bramson and Durrett (1988). For a model related to ours see the proof of Theorem 5 in Belhadji and Lanchier (2006) which holds for  $d = 1$ . Since we have in mind applications in  $d = 2$  and the proof is simpler (and less known) in  $d \geq 2$  we decided to skip the case  $d = 1$ .

As the next result shows, whether  $\phi$  is larger or smaller than 1 plays a critical role in the behavior of this model.

**Theorem 3.** *Assume that  $0 < \phi \leq 1$ . If  $N \geq 2d\lambda/\phi$  then, starting from any finite population, the population dies out for Model II on  $\mathbb{Z}^d$ .*

If the internal birth rate is less than 1 then excessive aggregation makes the species die out even in non catastrophic times.

Theorems 2 and 3 suggest the following conjecture. If  $\phi > 1$  then the survival probability in Model II increases with  $N$  while if  $\phi \leq 1$  then the survival probability decreases with  $N$ .

### 3. Proof of Theorem 2

There are two parts in our proof. In the first part we will show that if site  $x$  has  $N$  individuals and  $y$  is one of its  $2d$  nearest neighbors then  $x$  will eventually give birth to an individual in  $y$  that will, by internal births alone, generate  $N - 1$  individuals and therefore make  $y$  reach state  $N$ . Moreover, we will show that the probability of the preceding event converges to 1 as  $N$  goes to infinity. In the second part we will compare the process to a percolation model.

**First part.** To prove the first part we need three steps.

Step 1. Let  $x$  be a site in the lattice  $\mathbb{Z}^d$ . Assume that  $x$  is in state  $N$ . Let  $R_N$  be the number of times site  $x$  returns to state  $N$  before dropping for the first time to state 0. We show that as  $N$  goes to infinity the probability that  $\{R_N \geq N^2\}$  converges to 1. Moreover, we will show that this is true even if we ignore the external births (those with rate  $\lambda$ ) and only consider internal births (those with rate  $\phi$ ).

Assume that site  $x$  has  $i$  individuals at some time, where  $1 \leq i \leq N - 1$ . Then  $x$  goes to state  $i + 1$  at rate  $i\phi$  or to  $i - 1$  at rate  $i$ . Hence, ignoring possible births from the outside, the number of individuals at  $x$  is a simple random walk where

$$i \rightarrow i + 1 \text{ with probability } p = \frac{\phi}{\phi + 1} \text{ for } 1 \leq i \leq N - 1$$

$$i \rightarrow i - 1 \text{ with probability } q = \frac{1}{\phi + 1} \text{ for } 1 \leq i \leq N$$

The probability that, starting at  $N - 1$ , this random walk returns to  $N$  before reaching 0 is given by the classical ruin problem formula:

$$a(N, \phi) = \frac{1 - (q/p)^{N-1}}{1 - (q/p)^N}.$$

See, for instance, (4.4) in I.4 in Schinazi (1999). By the Markov property we have

$$P(R_N \geq r) = a(N, \phi)^r.$$

Using that  $a(N, \phi) > 1 - 2(q/p)^{N-1}$  we get

$$P(R_N \geq r) > \exp(-2r(q/p)^{N-1}).$$

Hence,

$$\lim_{N \rightarrow \infty} P(R_N \geq N^2) = 1,$$

where we use that since  $\phi > 1$ ,  $q < p$ . Of course, the limit above holds for any power of  $N$ .

Step 2. We show that since site  $x$  is likely to return to state  $N$  at least  $N^2$  times it will give birth on one of its  $2d$  neighbors  $y$  at least  $\sqrt{N}$  times. Let  $B_N$  be the number of births from site  $x$  to site  $y$ . We have

$$P(B_N \geq n) \geq P(B_N \geq n | R_N \geq N^2)P(R_N > N^2).$$

At each return to state  $N$  there are two possibilities either there is a birth from site  $x$  onto site  $y$  (at rate  $\lambda$ ) or there is a death at site  $x$  at rate  $N$ . Thus, the probability of a birth at  $y$  before a death at  $x$  is

$$\frac{\lambda}{\lambda + N}.$$

Moreover, at each return what happens is independent of what happened at the preceding return. Conditioning on  $\{R_N > N^2\}$  the number of births,  $B_N$ , from  $x$  onto  $y$  is therefore larger than a binomial random variable  $C_N$  with parameters  $N^2$  and  $\frac{\lambda}{\lambda+N}$ . For every real  $a > 0$  we have

$$\lim_{N \rightarrow \infty} \frac{\text{Var}(C_N)}{N^{1+2a}} = 0.$$

That is,

$$\frac{C_N - E(C_N)}{N^{1/2+a}}$$

converges to 0 in  $L^2$  and hence in probability. In particular,

$$\lim_{N \rightarrow \infty} P(C_N > E(C_N) - N^{1/2+a}) = 1.$$

By picking  $a$  in  $(0, 1/2)$  we get that

$$\lim_{N \rightarrow \infty} P(C_N > N^{1/2}) = 1.$$

Since,

$$\begin{aligned} P(B_N > N^{1/2}) &\geq P(B_N > N^{1/2} | R_N \geq N^2)P(R_N \geq N^2) \\ &\geq P(C_N > N^{1/2})P(R_N > N^2) \end{aligned}$$

and that each probability on the r.h.s. converges to 1 as  $N$  goes to infinity, we have

$$\lim_{N \rightarrow \infty} P(B_N > N^{1/2}) = 1.$$

Step 3. We show that given that there are at least  $N^{1/2}$  births at site  $y$ , at least one of these individuals generates, by internal births only,  $N - 1$  individuals so that  $y$  eventually reaches state  $N$ . Every time there is a birth at  $y$  it starts a birth and death chain with transition rates:

$$\begin{aligned} i &\rightarrow i + 1 \text{ at rate } i\phi \text{ for } i \geq 1 \\ i &\rightarrow i - 1 \text{ at rate } i \text{ for } i \geq 1 \end{aligned}$$

Since  $\phi > 1$ , this birth and death chain is transient (see for instance Proposition I.4.1 in Schinazi (1999)) and therefore there is a positive probability,  $q(\phi)$ , that starting in state 1 it will never be in state 0 and will go on to infinity.

Thus, the probability that site  $y$  will reach  $N$  in Model II is at least as large as the probability that one of the birth and death chains is transient.

For  $x$  and  $y$  nearest neighbors, let  $E_{xy}$  be the event that, given that  $x$  starts in state  $N$ , it gives birth to at least one individual on  $y$  whose associated birth and death chain is transient. We have

$$P(E_{xy}) \geq P(E_{x,y} | B_N > N^{1/2}) P(B_N > N^{1/2}) \geq (1 - (1 - q(\phi))^{N^{1/2}}) P(B_N > N^{1/2}).$$

As  $N$  goes to infinity  $P(E_{xy})$  approaches 1.

**Second part.** In this part we compare Model II to a percolation model. We follow closely Kuulasmaa (1982). Between any two nearest neighbors  $x$  and  $y$  in  $Z^d$  we draw a directed edge from  $x$  to  $y$ . We declare the directed edge open if the event  $E_{xy}$  happens. This defines a percolation model. Note that the probability of the directed edge  $xy$  be open is the same for all edges  $xy$  and can be made arbitrarily close to 1 by taking  $N$  large enough. By comparing this percolation model to a site percolation model it can be shown that there is a strictly positive probability of an infinite open path that starts at the origin of  $Z^d$ , provided the dimension  $d$  is at least 2. See the proof of Theorem 3.2 in Kuulasmaa (1982). It is important for this comparison to work that edges starting from different vertices are independently open. It is easy to check that if  $x \neq z$  then the events  $E_{xy}$  and  $E_{zt}$  are independent for any  $y$  and  $t$  nearest neighbors of  $x$  and  $z$ , respectively.

An infinite open path starting from the origin is one way for the population, started with  $N$  individuals at the origin, to survive forever. This completes the proof of Theorem 2.

### 4. Proof of Theorem 3

Assume that at a certain time we have a total population of  $n \geq 1$  individuals in Model II. The population may lose one individual or gain one. We start by examining the birth rate. Let  $k$ ,  $0 \leq k \leq n/N$ , be the number of sites with  $N$  individuals each, this accounts for  $kN$  individuals. The other  $n - kN$  individuals are in sites where there are  $N - 1$  or less individuals per site.

If site  $x$  is in state  $N$  then it gives birth on nearest neighbor  $y$  with rate  $\lambda$ , provided  $y$  is not in state  $N$ . Since there are  $2d$  nearest neighbors the birth rate from a site with  $N$  individuals is at most  $2d\lambda$ . The other  $n - kN$  individuals all give birth with rate  $\phi$ . Thus, the total birth rate for  $n$  individuals occupying  $k$  sites in Model II is at most

$$2d\lambda k + (n - kN)\phi = k(2d\lambda - N\phi) + n\phi \leq n\phi$$

since we assume that  $2d\lambda \leq N\phi$ .

The death rate for  $n$  individuals is  $n$ .

Consider now the birth and death chain with the following rates

$$\begin{aligned} n &\rightarrow n + 1 \text{ at rate } n\phi \text{ for } n \geq 1, \\ n &\rightarrow n - 1 \text{ at rate } n \text{ for } n \geq 1. \end{aligned}$$

The total birth rate in Model II is less than this birth rate and the total death rate is the same. Hence, if this birth and death chain dies out with probability 1 so does the population in Model II. It is well known that this birth and death chain dies out if and only if  $\phi \leq 1$  (see for instance Schinazi (1999)). This concludes the proof of Theorem 3.

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