The Stochastic Metapopulation Model

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July 18, 2015

1 Introduction

The metapopulation model was first described as a *population of populations* by Richard Levins in 1970 (Hanski and Gilpin, 1991). In Levins formulation, he proposed a differential equation to model the proportion, p, of habitat patches occupied by a species. This formulation was significant step forward in population ecology. The model turned the focus of dynamics on a single local population to include dynamics of immigration and extinction events between several populations sites (Gotelli, 1990). This connected the traditionally separate studies of local population ecology (changes in abundance over time) and regional biogeography (occurrence and distribution over space).

In examining Levins' metapopulation model as a stochastic process, it is useful to reformulate the metapopulation model in terms of the number of patches occupied, n. First, the total number of patches that exist needs to be defined. We can refer to this total number of patches as h. This allows us to model the changes in metapopulation in discrete integer intervals, whereas Levins' formulation would require changes to be fractional, which can be tricky to deal with as a stochastic process. Also, in reformulating the model in terms of n, the model can be compared to the logistic growth model. Both formulations of the metapopulation differential equation can be rewritten so that their forms match the form of the logistic growth differential equation

Lastly, I will talk about how the stochastic models do produce reasonable output and how a scaling factor is required to match the timescales between the deterministic model and the stochastic model.

2 Deterministic Model

Levins' original formulation of the metapopulation model includes two important parameters: i and e. The immigration rate i describes the rate of movement of existing populations to new unoccupied patches while the e describes the extinction rate of current populations. The differential equation is as follows

$$\frac{dp}{dt} = ip(1-p) - ep \tag{1}$$

This describes a system where 1.) populations in occupied patches colonize unoccupied patches and 2.) populations in some patches go extinct and create unoccupied patches. The rates of these events depends on the current proportion of occupied patches. This differential equation can be graphed given parameter values and an initial proportion value, p_0. Suppose $i = 0.08$, $e = 0.02$, and $p_0 = 0.01$. The solution will look like:

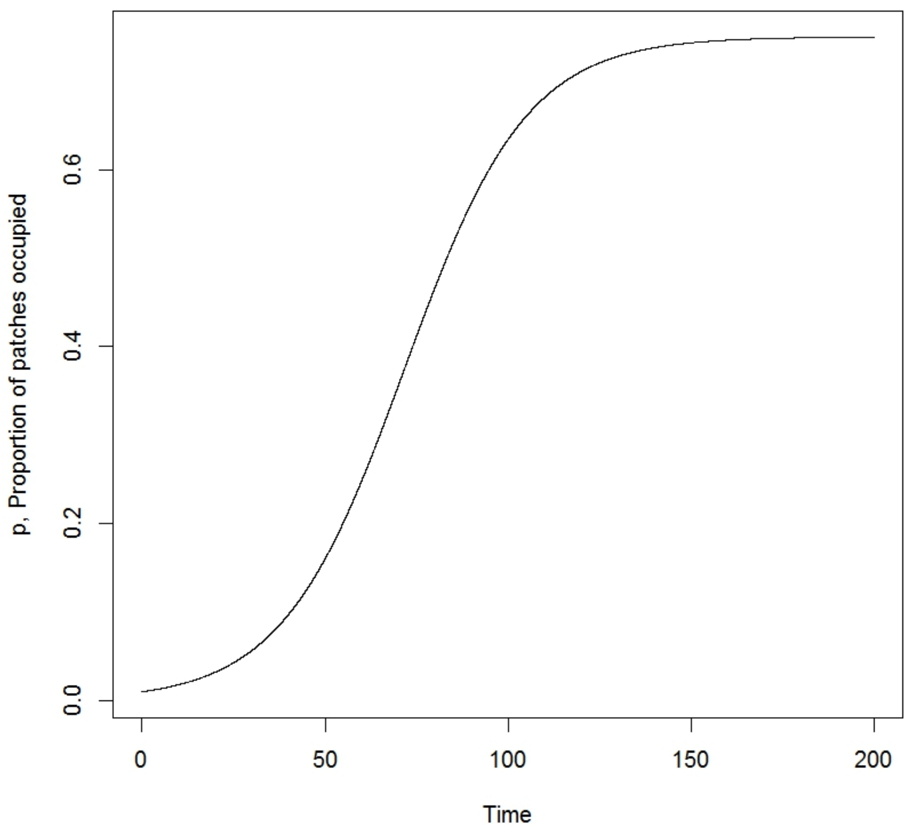

Figure 1: Solution for the Metapopulation model with parameters $i = 0.08$, $e = 0.02$, and $p_0 = 0.01$

This model can be rewritten in terms of n, the number of patches occupied. The relationship between p, n, and h is $p = \frac{n}{h}$. If we substitute n/h for p in Levins' differential equations, we get

$$\frac{dn}{dt} = in(1 - \frac{n}{h}) - en \tag{2}$$

This can be modelled with the same parameters, with the exception that the new parameter h must be defined. If we define h as 200, the solution will look similar except that the y-axis is scaled up by a factor of 200.

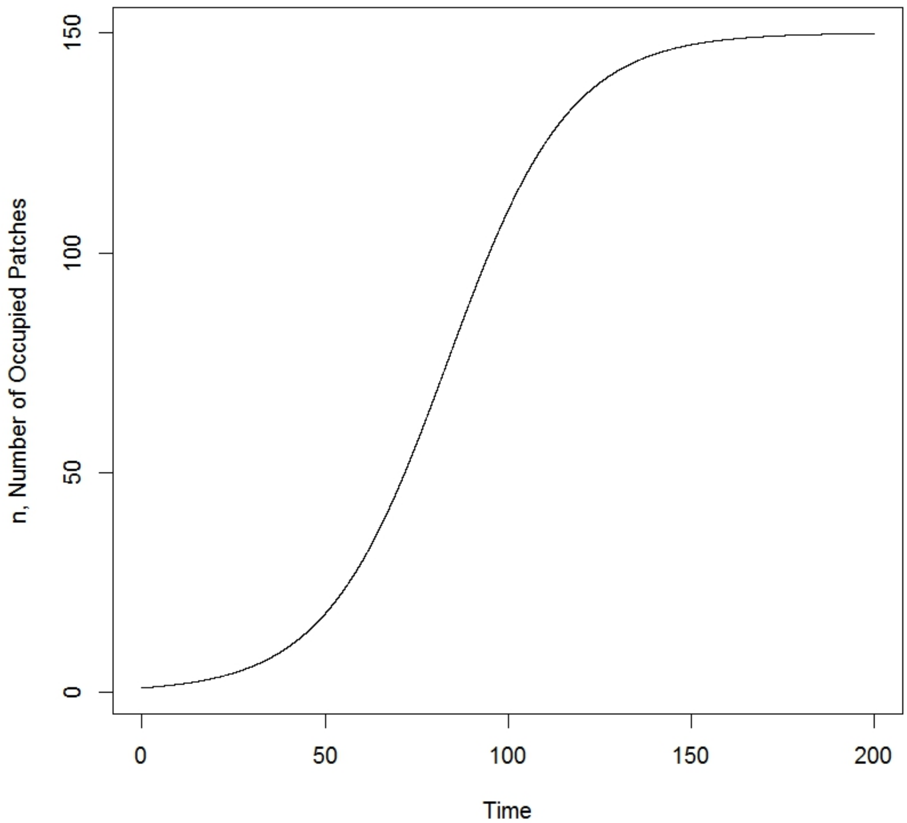

Figure 2: Solution for the Metapopulation model with parameters $i = 0.08$, $e = 0.02$, and $p_0 = 0.01$

This looks very similar to the Logistic Growth model with carrying capacity 150 and rate 0.06. In fact, the metapopulation formula can be rewritten to match the structure of the logistic growth model. The logistic growth equation (3) and the metapopulation equation (4) can be juxtaposed to see their similarities; and the appropriate parameters should match as follows.

$$\frac{dn}{dt} = rn(1 - \frac{n}{k}) \tag{3}$$

$$\frac{dn}{dt} = (i - e)n(1 - \frac{in}{(i - e)h}) \tag{4}$$

$$r = i - e \tag{5}$$

$$k = \frac{h(i - e)}{i} \tag{6}$$

In terms of the logistic growth model, the rate r is analogous to the difference of the immigration and extinction rates, while the carrying capacity k is analogous to the equilibrial proportion of the total number of patches. Graphing the logistic model with $k = 150$ and

$r = 0.06$ exactly matches the last graph of the metapopulation model. This makes sense since $r = i - e = 0.08 - 0.02 = 0.06$) and $k = h(i-e)/i = 200 * 0.06/0.08 = 150$.

3 Stochastic Model

The metapopulation model can be simulated stochastically in terms of p, the proportion of sites occupied, or n, the number of patches occupied. In the deterministic model, we saw that the graph for modelling n (Figure 2), simply scales the y-axis for the graph of p (Figure 1). As one would expect, simulating the n formulation of the model and scaling the y-axis down would create a simulation that matches our solution for p (Figure1).

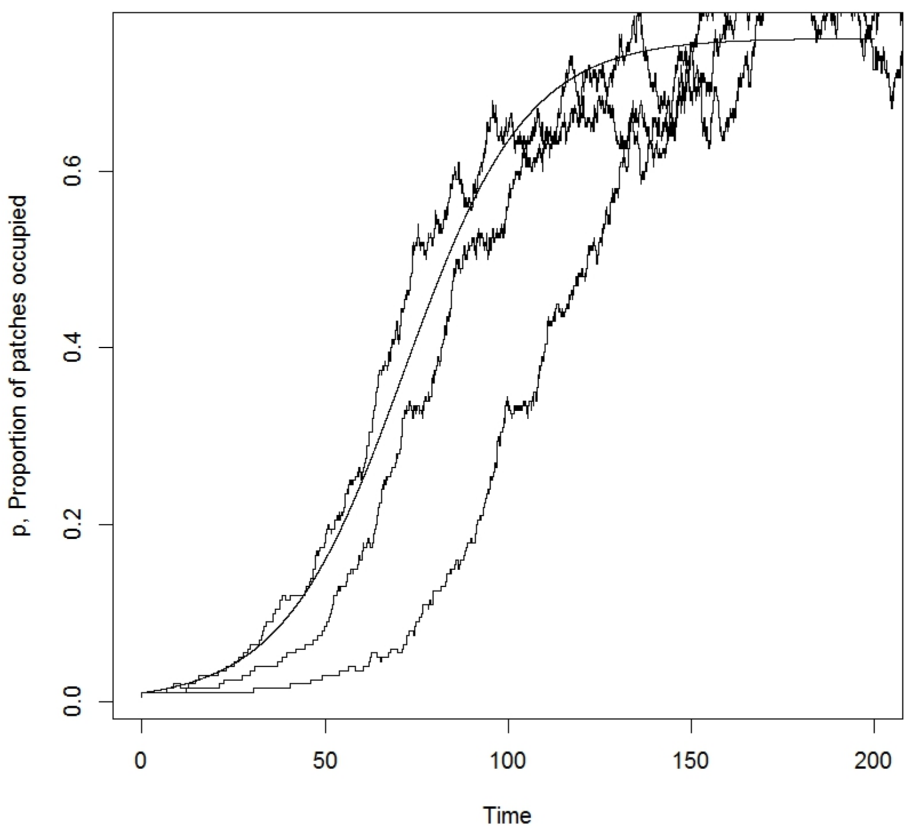

Figure 3: Stochastic Simulations for the number of patches occupied, scaled down by a factor of 200, with Figure 1 in the background.

Simulating Levins' formulation of the metapopulation model was trickier. This formulation is unlike the stochastic simulations of the logistic growth model or simulations of simple birth and death processes, where the states are defined in discrete integer intervals i.e. 1, 2, 3,.... By using p, the proportion of occupied patches, the range of the states is limited between 0 and 1. The states inbetween 0 and 1 aren't as clearly defined, making it a little more difficult to interpret how the proportion would increase or decrease for each stochastic event.

After playing around with a stochastic version of Levins' model, I figured out that the step size, s, between events could be defined by the user, or in more biological terms, it could be defined as one over the total number of possible patches, i.e. $s = 1/h$. After choosing this amount, I found that the interevent times were much larger than expected and did not create simulations that matched the deterministic model. After trying different values, the value that scaled the time axis the best was $s = 1/h$. I tested the values $s = 1/50 = 0.02$ and $s = 1/1000 = 0.001$. This resulted in accurate stochastic simulations, where jumps in proportion and time were coarse for $h = 50$ and were fine when using $h = 1000$.

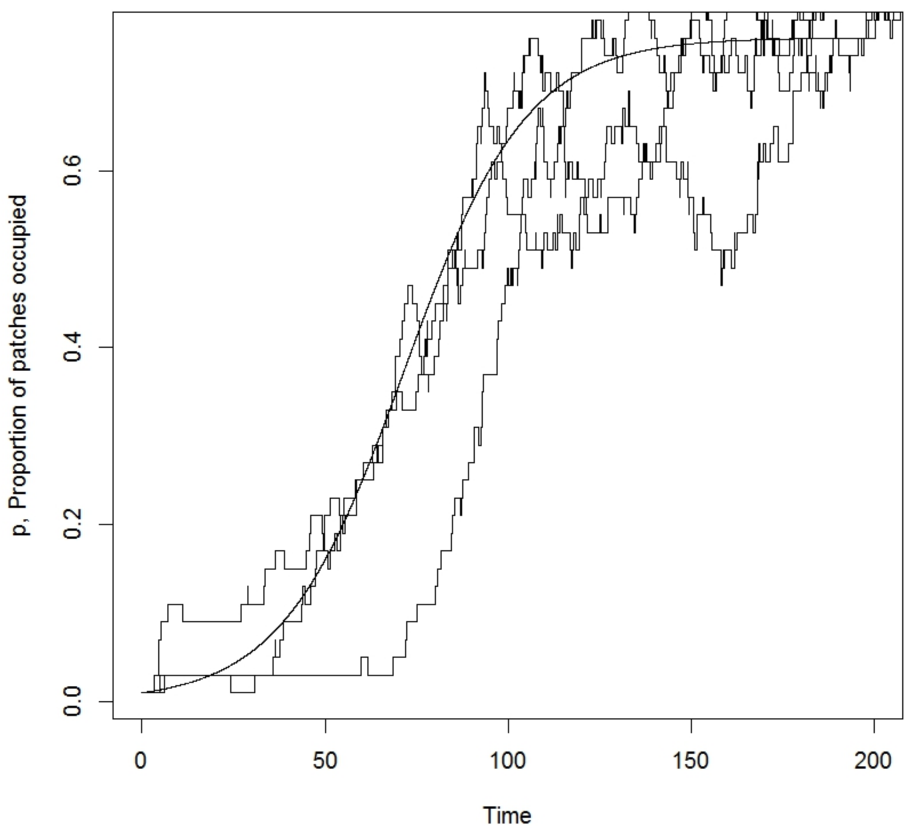

Figure 4: Stochastic Simulations for the proportion of patches occupied, using step size of 0.02, with Figure 1 in the background.

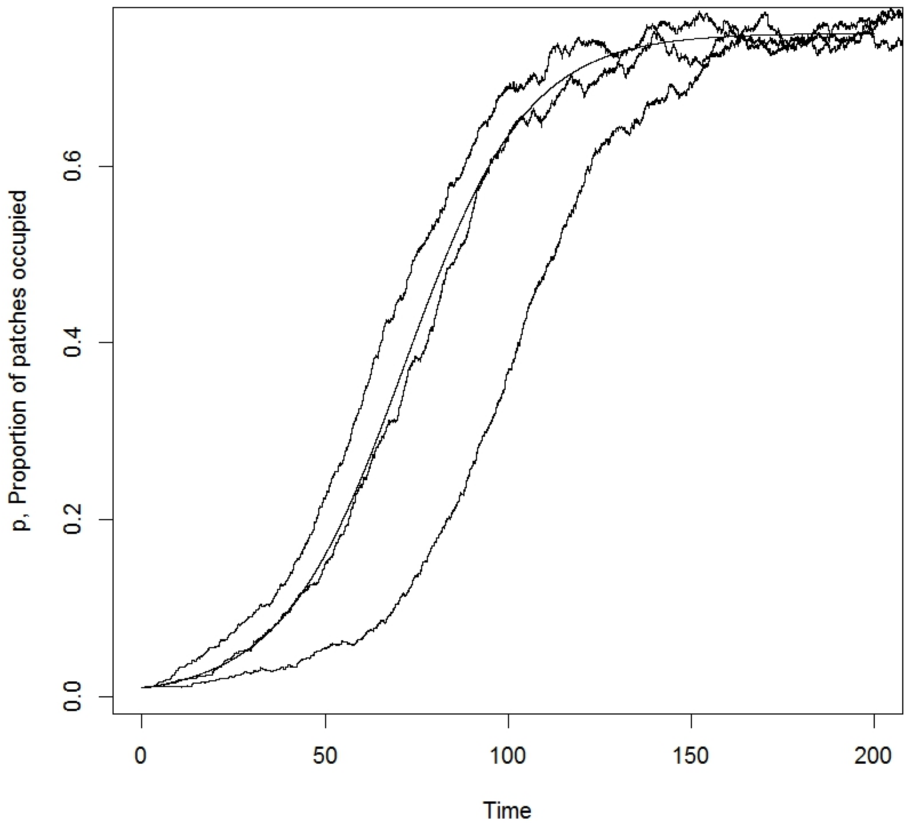

Figure 5: Stochastic Simulations for the proportion of patches occupied, using step size of 0.001, with Figure 1 in the background.

The resulting equation for interevent time was

$$T_i = -s\frac{ln(U)}{\alpha(n)} \tag{7}$$

It is interesting that stochastic processes are easily interpreted and modeled when the events are associated with an integer change between population states, i.e., the population increases or decreases by one. After searching through many dynamic models, especially in physics, I was discouraged because modeling an increments in decimal amounts is not as clear as simply adding or subtracting one to a population. I now see that these processes, such as the dynamics of a mass on a spring, can be simulated if the interevent time is scaled by the increment chosen.

4 Code

```
####To graph the Differential Equation#####
parameters<-c(i=0.08, e=0.02)
state<-c(P=0.01)

Metapop<-function(t, state, parameters) {
 with(as.list(c(state, parameters)),{
 # rate of change
 dP<-i*P*(1-P)-e*P

 # return the rate of change
 list(c(dP))
 }) # end with(as.list...
 }


times<-seq(0,200,by=0.01)


out <- as.data.frame(ode(y=state,times=times,func=Metapop,parms=parameters))

plot(times,out$P,type="l",xlab="Time",ylab="p, Proportion of patches occupied")



########To graph the logistic equation and scaled down to be proportional abundance##

N<-c(1,0)
k<-150
t<-c(0,0)
r<-0.06

birth<-function(N){r*N}
death<-function(N){r*N^2/k}

for(j in 1:3){


for(i in 1:10000){
t[i+1]<-t[i]-log(runif(1))/(birth(N[i])+death(N[i]))

if( runif(1) < ( birth(N[i])/(birth(N[i])+ death(N[i]) ) ) ){
N[i+1]=N[i]+1
}else{
N[i+1]=N[i]-1
}
```

```
}
lines(t,N/200,type="S")
}


####To graph the actual Levins model as a stochastic process####

i<-0.08
e<-0.02
x0<-0.01

inc<-function(p){ i*p*(1-p)}
dec<-function(p){e*p}
growth<-function(p){inc(p)+dec(p)}

for(j in 1:3){

t<-c(0,0)
p<-c(x0,x0)

for(k in 1:10000){
rate<-growth(p[k])
t[k+1]<-t[k]-log(runif(1))/rate*(0.001)

if(runif(1)< (inc(p[k])/rate)){p[k+1]<-p[k]+0.001
}else{p[k+1]<-p[k]-0.001}
}
lines(t,p,type="s")

}
```

References

Gotelli, N. J. (1990). Metapopulation models: The rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist 138*(3).

Hanski, I. and M. Gilpin (1991). Metapopulation dynamies: brief history and conceptual domain. *Biological Journal of the Linnean Society 42*, 3–16.