Report of Assignment 2

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1, Introduction

Description of the original paper

Previous models imposed environmental conditions, like spatial structured population (put individuals into different groups) to favor cooperative individuals. This paper added a new trait of deciding which group to join beyond the cooperative/selfish trait to examine if the cooperative individuals are still favored. This trait that affects the environment is called niche construction.
The paper began with a preliminary experiment to determine the suitable sizes for the large and small groups. By plotting and observing the parameter space of the group sizes and reproduction generations in the groups, it was decided to set the value at 4 and 40 for the small and large groups respectively.
Then the paper made pairwise comparisons of the frequencies of all the 4 genotypes at equilibrium. The expected result is selfish+large > cooperative+large > cooperative+small > selfish+small, and the population was expected to evolve to selfish+large at fixation.
However, the next experimental results were not as expected. The frequencies of individuals with large and selfish trait increased at the beginning, but then quickly dropped. The individuals of cooperative+small became dominant at equilibrium.

Representation of an individual

In my program, the individual was represented by a data structure of Python dictionary with key value form:
{'trait1':'small','trait2':'selfish'}
{'trait1':'small','trait2':'cooperative'}
{'trait1':'large','trait2':'selfish'}
{'trait1':'large','trait2':'cooperative'}

Fitness function

No fitness function defined to map one genotype to a specific value in this paper and my Python program. But there was a growth equation (defined in the paper) to calculate the number of individuals in different genotypes within groups. The growth rate represented by different parameters and final size after reproduction of each genotype reflect its different adaptability.

Genetic algorithm

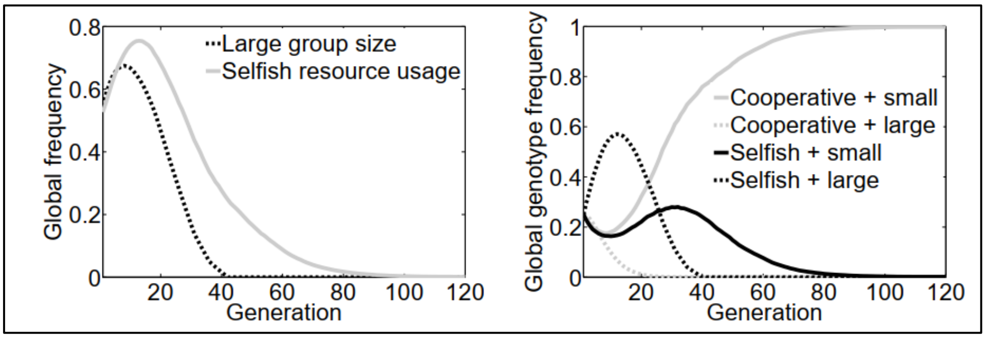
The algorithm used in this paper is a generational genetic algorithm with group selection. The group selection works like fitness proportionate selection when the pool was rescaled into original size according to the frequencies' proportion of the genotypes after reproduction within groups in every generation. The difference is the group selection proceed by the frequencies of genotypes but the fitness proportionate selection proceeds by the value of fitness.

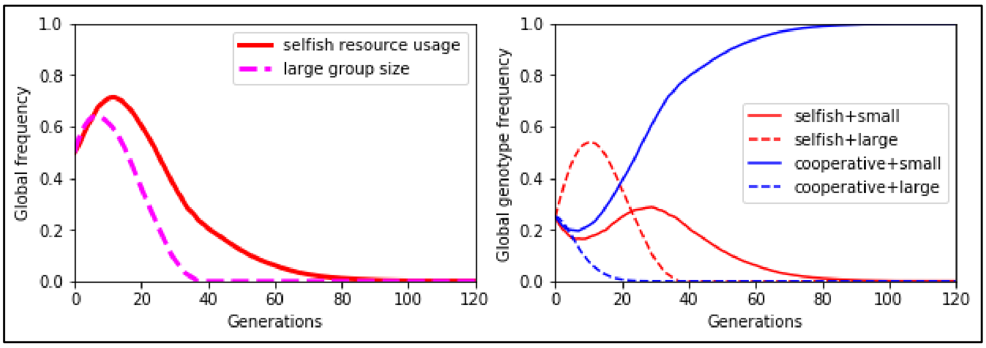
All parameters

Parameter	Value
Growth rate (cooperative), G_c	0.018
Growth rate (selfish), G_s	0.02
Consumption rate (cooperative), C_c	0.1
Consumption rate (selfish), C_s	0.2
Population size, N	4000 (1000 individuals each genotype)
Number of generations, T	1000
Time-steps that reproduction performed within groups, t	4
Death rate to all genotypes, K	0.1
Group's resource influx, R	4(small),50(large)
Size of small groups, S	4(small),40(large)

2, Reimplemented Results

The reimplemented figures





The cooperative/selfish trait was distinguished by different colors: red-selfish, blue-cooperative. The 'large' line in left plot is in magenta(=red+blue), because it consists of large +selfish(red) and large +cooperative(blue). On the large/small trait, it was distinguished by the shape of line: solid-small, dotted-large.

Discussion of the results

The plots above demonstrated the power of spatial structure and niche construction, it protected the cooperative individuals in the separative small groups and made them take advantage of competition between groups. It finally prompted them to win at equilibrium.

3, Extension

Research question

In this extension, I will explore the effect of mutation on the frequency of different genotypes in this scenario. The mutation here means that individuals with cooperative trait mutate into individuals with selfish trait during the reproduction within the groups.

Description of methods

In the case of mutation, the number of individuals in the group with genotype i changes according to:

$$n_i(t) = n_i(t-1) + \frac{r_i}{C_i} - Kn_i(t-1) + mu, \qquad mu = \begin{cases} M, if\ i = selfish \\ -M, if\ i = cooperative \end{cases}$$

Where M is the number of mutant individuals in the t generation. Compare to the equation in the original paper, the selfish population gets additional individual mutated from the cooperative population, at the same time the cooperative population loses the same number of individuals.

The pseudocode below shows how to calculate M:

```
mu_list=[ ]
for i from 1 to size (n_i(t))
   if rand()<mu_rate  then
      mu_list.append(i)
M=size(mu_list)
```

In order to compare the effect of different mutation rate, it is defined in the pseudocode as:

$$mu\_rate = \frac{1}{m * n_i(t)}$$

where *m* is the coefficient to control the size of mutation rate, the larger the m, the smaller the mutation rate. And $n_i(t)$ is the number of individuals in the groups with genotype i as described in the original paper. Since the mutation happened only from cooperative individuals to selfish individuals, the genotype i here refers to cooperation.

The value of the research question

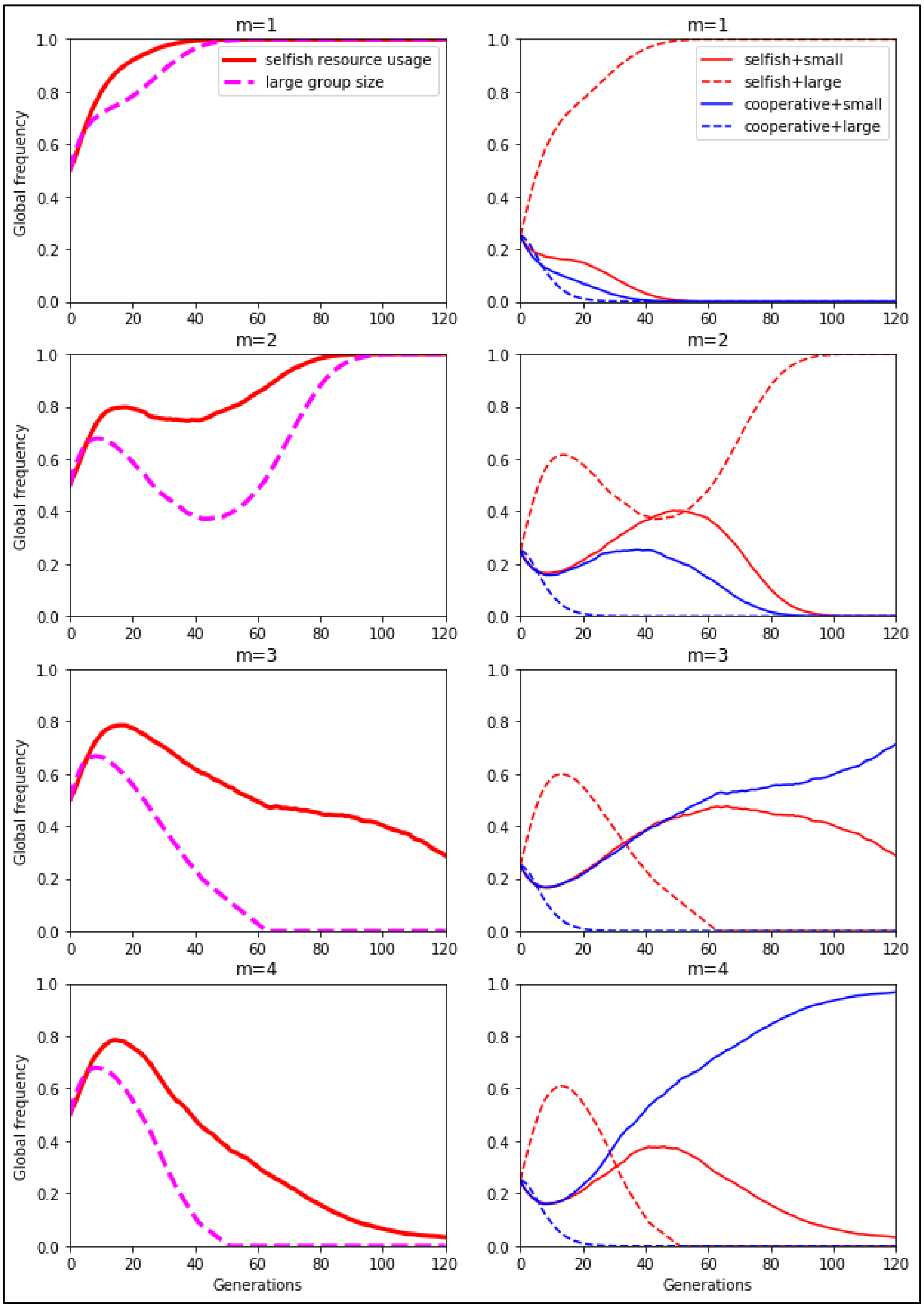
Inspired by the end of the original paper i.e., the 'future work' part, I decided to examine whether the environment still prefers cooperative trait or the degree of preference under the stress of mutation.

Expected results

Since the mutation is bad for the cooperative individuals and good for the selfish individuals, I expected the increase of frequency of cooperative individuals will slow down and even outcompeted by the selfish individuals at the equilibrium state as the mutation rate increase.

4, Results of extension

The plots below show the frequencies of each genotypes at different values of *m*. As the *m* becomes larger the mutation rate becomes smaller and the impact on the frequency of each genotype becomes smaller. When m=4, the mutation rate becomes so small that the changes in genotype frequency over generations are almost like the result in the original paper.



5, Conclusion

No matter what's the value of mutation rate, the large groups always favor selfish individuals than cooperative individuals. The change of cooperative+large individuals died out quickly everytime, and the mutation made this situation even worse.

However, the small groups favor cooperative individuals than selfish individuals only when the mutation rate is relatively small(m=3,4), otherwise the obstruction of mutation will offset cooperative individuals' comparative advantage between groups.

The process of inhibiting cooperative individuals by mutation happened during the reproduction in the groups. The reason why cooperative individuals couldn't win under some degree of mutation is there was not enough variation in final group sizes before mixing. The variation that should have been caused by the original reproduction mechanism was reduced by the mutation in a way that promoting the selfish individuals and inhibiting the cooperative individuals. As a result, the cooperative individuals were no longer favored by the group selection regardless of the power of niche construction when the mutation rate reaches a certain level.

6, Appendix

```
# 1,Initialisation:Initialise the migrant pool with N individuals.
def initialization(n1,n2,n3,n4):
    p1=[{'trait1':'small','trait2':'selfish'}]*n1
    p2=[{'trait1':'large','trait2':'selfish'}]*n2
    p3=[{'trait1':'small','trait2':'cooperative'}]*n3
    p4=[{'trait1':'large','trait2':'cooperative'}]*n4
    return p1+p2+p3+p4
```

```
#2,Group formation (aggregation): Assign individuals in the migrant pool to groups
def assign_groups(groups,population,size):
    import random
    if len(population)<size and len(population)>0:
        #print('not enough individuals for sampling')
        return []
    elif len(population)>=size:
        index_value = random.sample(list(enumerate(population)), size)
        sample_idx = []
        sample = []
        for idx, val in index_value:
            sample_idx.append(idx)
            sample.append(val)
        groups.append(sample)
        population1=[i for j, i in enumerate(population) if j not in sample_idx]
        #print(population1) #test if the population decreased after sampling without replacement
        assign_groups(groups,population1,size)
        #print(len(population1)<size)#print the boolean value in every recursion
    return groups
```

```
#3,Reproduction: Perform reproduction within groups for t time-steps
def reproduction(t,group,Gs,Cs,Gc,Cc,K,R):
    if t==0:
        Ns_0=sum(1 for i in group if i['trait2']=='selfish')
        Nc_0=sum(1 for i in group if i['trait2']=='cooperative')
        return Ns_0,Nc_0
    else:
        Ns_last,Nc_last=reproduction(t-1,group,Gs,Cs,Gc,Cc,K,R)
        rs=(Ns_last*Gs*Cs*R)/(Ns_last*Gs*Cs+Nc_last*Gc*Cc)
        rc=(Nc_last*Gc*Cc*R)/(Ns_last*Gs*Cs+Nc_last*Gc*Cc)
        Ns_t=Ns_last+rs/Cs-K*Ns_last
        Nc_t=Nc_last+rc/Cc-K*Nc_last

    return Ns_t,Nc_t
```

```
#4,Migrant pool formation (dispersal): Return the progeny of each group to the migrant pool.
def dispersal(g_snew,g_lnew):
    pool1=[]
    for i in g_snew:
        pool1=pool1+i

    pool2=[]
    for i in g_lnew:
        pool2=pool2+i
    pool=pool1+pool2
    return pool
```

```
#5,Maintaining the global carrying capacity: Rescale the migrant pool back to size N,
#retaining the proportion of individuals with each genotype
def rescale(pool,initial_p):
    n1=round(sum(1 for i in pool if i['trait1']=='small' and i['trait2']=='selfish')*initial_p/len(pool))
    n2=round(sum(1 for i in pool if i['trait1']=='large' and i['trait2']=='selfish')*initial_p/len(pool))
    n3=round(sum(1 for i in pool if i['trait1']=='small' and i['trait2']=='cooperative')*initial_p/len(pool))
    n4=round(sum(1 for i in pool if i['trait1']=='large' and i['trait2']=='cooperative')*initial_p/len(pool))
    p=[{'trait1':'small','trait2':'selfish'}]*n1+[{'trait1':'large','trait2':'selfish'}]*n2+[{'trait1':'small','trait2':'cooperative'}]*n3+[{'
    return p,n1/initial_p,n2/initial_p,n3/initial_p,n4/initial_p
```

```
#6,Iteration
#1,initialization
i1,i2,i3,i4=1000,1000,1000,1000
i=i1+i2+i3+i4
p=initialization(i1,i2,i3,i4)
Selfish,Large=[(i1+i2)/i],[(i2+i4)/i]#for calculating number of selfish strategy individuals and large groups
Generation,N1,N2,N3,N4=[0],[i1/i],[i2/i],[i3/i],[i4/i]#for calculating the frequency of each genotype
```

```
for iteration in range(120):
    #2,Group Formation
    p_s=[i for i in p if i['trait1']=='small']#individuals with trait1 value of 'small'
    p_l=[i for i in p if i['trait1']=='large']#individuals with trait1 value of 'large'
    g_s=assign_groups([],p_s,4)#small groups
    g_l=assign_groups([],p_l,40)#large groups
    #3,Reproduction
    g_snew=[]
    for group in g_s:
        Ns_t=round(reproduction(4,group,0.02,0.2,0.018,0.1,0.1,4)[0])
        Nc_t=round(reproduction(4,group,0.02,0.2,0.018,0.1,0.1,4)[1])
        group_new=[{'trait1':'small','trait2':'selfish'}]*Ns_t+[{'trait1':'small','trait2':'cooperative'}]*Nc_t
        g_snew.append(group_new)
    g_lnew=[]
    for group in g_l:
        Ns_t=round(reproduction(4,group,0.02,0.2,0.018,0.1,0.1,50)[0])
        Nc_t=round(reproduction(4,group,0.02,0.2,0.018,0.1,0.1,50)[1])
        group_new=[{'trait1':'large','trait2':'selfish'}]*Ns_t+[{'trait1':'large','trait2':'cooperative'}]*Nc_t
        g_lnew.append(group_new)
    #4,Migrant pool formation
    pool=dispersal(g_snew,g_lnew)
    #5,Rescale the migrant pool back to size N
    p=rescale(pool,i)[0]
    Generation.append(iteration+1)
    N1.append(rescale(pool,i)[1])
    N2.append(rescale(pool,i)[2])
    N3.append(rescale(pool,i)[3])
    N4.append(rescale(pool,i)[4])
    Selfish.append(rescale(pool,i)[1]+rescale(pool,i)[2])
    Large.append((sum(len(g) for g in g_lnew))/(sum(len(g) for g in g_lnew)+sum(len(g) for g in g_snew)))
```

```
#Plots
import matplotlib.pyplot as plt
fig, (ax1, ax2) = plt.subplots(1, 2,figsize=(10,3))

ax1.plot(Generation, Selfish, label = "selfish resource usage",color='red', linewidth=3)
ax1.plot(Generation, Large, '--',label = "large group size",color='magenta', linewidth=3) #blue+red=magenta

ax1.set(xlabel='Generations', ylabel='Global frequency')
ax1.set_xlim([0, 120])
ax1.set_ylim([0, 1])
ax1.legend()

ax2.plot(Generation, N1, label = "selfish+small",color='red')
ax2.plot(Generation, N2, '--',label = "selfish+large",color='red')
ax2.plot(Generation, N3, label = "cooperative+small",color='blue')
ax2.plot(Generation, N4, '--',label = "cooperative+large",color='blue')

ax2.set(xlabel='Generations', ylabel='Global genotype frequency')
ax2.set_xlim([0, 120])
ax2.set_ylim([0, 1])
ax2.legend()
```

```
#Extension: introduce mutation
def reproduction_m(t,group,Gs,Cs,Gc,Cc,K,R,m):
    import random
    if t==0:
        Ns_0=sum(1 for i in group if i['trait2']=='selfish')
        Nc_0=sum(1 for i in group if i['trait2']=='cooperative')
        return Ns_0,Nc_0
    else:
        Ns_last,Nc_last=reproduction(t-1,group,Gs,Cs,Gc,Cc,K,R)


        rs=(Ns_last*Gs*Cs*R)/(Ns_last*Gs*Cs+Nc_last*Gc*Cc)
        rc=(Nc_last*Gc*Cc*R)/(Ns_last*Gs*Cs+Nc_last*Gc*Cc)
        Ns_t=Ns_last+rs/Cs-K*Ns_last
        Nc_t=Nc_last+rc/Cc-K*Nc_last
        mu=[]
        for i in range(round(Nc_t)):
            if random.uniform(0, 1)<1/(m*Nc_t):
                mu.append(i)
        Ns_t=Ns_t+len(mu)
        Nc_t=Nc_t-len(mu)
    return Ns_t,Nc_t
```

```
GG,NN1,NN2,NN3,NN4,SS,LL=[],[],[],[],[],[],[]
for m in range(1,10):
#for m in [1,2,3,4,5,6,0.2,0.4,0.6,0.8]:
    #1,initialization
    i1,i2,i3,i4=1000,1000,1000,1000
    i=i1+i2+i3+i4
    p=initialization(i1,i2,i3,i4)
    Selfish,Large=[(i1+i2)/i],[(i2+i4)/i]#for calculating number of selfish strategy individuals and large groups
    Generation,N1,N2,N3,N4=[0],[i1/i],[i2/i],[i3/i],[i4/i]#for calculating the frequency of each genotype
```

```python
    for iteration in range(120):
        #2.Group Formation
        p_s=[i for i in p if i['trait1']=='small']#individuals with trait1 value of 'small'
        p_l=[i for i in p if i['trait1']=='large']#individuals with trait1 value of 'large'

        g_s=assign_groups([],p_s,4)#small groups
        g_l=assign_groups([],p_l,40)#large groups
        #3.Reproduction
        g_snew=[]
        for group in g_s:
            Ns_t=round(reproduction_m(4,group,0.02,0.2,0.018,0.1,0.1,4,m)[0])
            Nc_t=round(reproduction_m(4,group,0.02,0.2,0.018,0.1,0.1,4,m)[1])
            group_new=[{'trait1':'small','trait2':'selfish'}]*Ns_t+[{'trait1':'small','trait2':'cooperative'}]*Nc_t
            g_snew.append(group_new)
        g_lnew=[]
        for group in g_l:
            Ns_t=round(reproduction_m(4,group,0.02,0.2,0.018,0.1,0.1,50,m)[0])
            Nc_t=round(reproduction_m(4,group,0.02,0.2,0.018,0.1,0.1,50,m)[1])
            group_new=[{'trait1':'large','trait2':'selfish'}]*Ns_t+[{'trait1':'large','trait2':'cooperative'}]*Nc_t
            g_lnew.append(group_new)
        #4.Migrant pool formation
        pool=dispersal(g_snew,g_lnew)
        #5.Rescale the migrant pool back to size N
        p=rescale(pool,i)[0]
        Generation.append(iteration+1)
        N1.append(rescale(pool,i)[1])
        N2.append(rescale(pool,i)[2])
        N3.append(rescale(pool,i)[3])
        N4.append(rescale(pool,i)[4])
        Selfish.append(rescale(pool,i)[1]+rescale(pool,i)[2])
        Large.append((sum(len(g) for g in g_lnew))/(sum(len(g) for g in g_lnew)+sum(len(g) for g in g_snew)))
    GG.append(Generation);NN1.append(N1);NN2.append(N2);NN3.append(N3);NN4.append(N4);SS.append(Selfish);LL.append(Large)
```

```python
import matplotlib.pyplot as plt
fig, ([ax1, ax2], [ax3, ax4], [ax5, ax6], [ax7, ax8]) = plt.subplots(4, 2,figsize=(10,15))

ax1.plot(GG[0], SS[0], label = "selfish resource usage",color='red', linewidth=3)
ax1.plot(GG[0], LL[0], '--',label = "large group size",color='magenta', linewidth=3) #blue+red=magenta
ax1.set(ylabel='Global frequency');ax1.set_xlim([0, 120]);ax1.set_ylim([0, 1]);ax1.legend();ax1.title.set_text('m=1')

ax2.plot(GG[0], NN1[0], label = "selfish+small",color='red')
ax2.plot(GG[0], NN2[0], '--',label = "selfish+large",color='red')
ax2.plot(GG[0], NN3[0], label = "cooperative+small",color='blue')
ax2.plot(GG[0], NN4[0], '--',label = "cooperative+large",color='blue')
ax2.set_xlim([0, 120]);ax2.set_ylim([0, 1]);ax2.legend() ;ax2.title.set_text('m=1')


ax3.plot(GG[1], SS[1], label = "selfish resource usage",color='red', linewidth=3)
ax3.plot(GG[1], LL[1], '--',label = "large group size",color='magenta', linewidth=3) #blue+red=magenta
ax3.set(ylabel='Global frequency');ax3.set_xlim([0, 120]);ax3.set_ylim([0, 1]);ax3.title.set_text('m=2')

ax4.plot(GG[1], NN1[1], label = "selfish+small",color='red')
ax4.plot(GG[1], NN2[1], '--',label = "selfish+large",color='red')
ax4.plot(GG[1], NN3[1], label = "cooperative+small",color='blue')
ax4.plot(GG[1], NN4[1], '--',label = "cooperative+large",color='blue')
ax4.set_xlim([0, 120]);ax4.set_ylim([0, 1]);ax4.title.set_text('m=2')
```

```python
ax5.plot(GG[2], SS[2], label = "selfish resource usage",color='red', linewidth=3)
ax5.plot(GG[2], LL[2], '--',label = "large group size",color='magenta', linewidth=3) #blue+red=magenta
ax5.set(ylabel='Global frequency');ax5.set_xlim([0, 120]);ax5.set_ylim([0, 1]);ax5.title.set_text('m=3')

ax6.plot(GG[2], NN1[2], label = "selfish+small",color='red')
ax6.plot(GG[2], NN2[2], '--',label = "selfish+large",color='red')
ax6.plot(GG[2], NN3[2], label = "cooperative+small",color='blue')
ax6.plot(GG[2], NN4[2], '--',label = "cooperative+large",color='blue')
ax6.set_xlim([0, 120]);ax6.set_ylim([0, 1]);ax6.title.set_text('m=3')


ax7.plot(GG[3], SS[3], label = "selfish resource usage",color='red', linewidth=3)
ax7.plot(GG[3], LL[3], '--',label = "large group size",color='magenta', linewidth=3) #blue+red=magenta
ax7.set(xlabel='Generations', ylabel='Global frequency');ax7.set_xlim([0, 120]);ax7.set_ylim([0, 1]);ax7.title.set_text('m=4')

ax8.plot(GG[3], NN1[3], label = "selfish+small",color='red')
ax8.plot(GG[3], NN2[3], '--',label = "selfish+large",color='red')
ax8.plot(GG[3], NN3[3], label = "cooperative+small",color='blue')
ax8.plot(GG[3], NN4[3], '--',label = "cooperative+large",color='blue')
ax8.set(xlabel='Generations');ax8.set_xlim([0, 120]);ax8.set_ylim([0, 1]);ax8.title.set_text('m=4')
```