Ecography

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Yackulic, C. B. 2016. Competitive exclusion over broad spatial extents is a slow process: evidence and implications for species distribution modeling. – Ecography doi: 10.1111/ecog.02836

Supplementary material

Appendix 1: Derivation of results presented in figures 1 and 2.

Figure A1 - Equilibrium occupancies of two competing species as a function of the prevalence of habitat favored by species 1. We assumed eight possible states and kept track of the proportion of sites expected to be in each of these states. The first four states corresponded to sites that were of the habitat preferred by species 1, and could be either empty (state 1), occupied by species 1 only (state 2), occupied by species 2 only (state 3) or occupied by both species (state 4). States 5-8 consisted of sites with the habitat preferred by species 2 and the same occupancy statuses as states 1-4 (i.e., state 5 was empty, state 6 was occupied by species 1 only, *etc.).* A transition matrix was constructed that allowed sites to transition with respect to occupancy states, but did not allow habitat transitions. Transition probabilities between occupancy states within a habitat can be decomposed in terms of colonization and extinction rates. The probability of colonization for species *j* between time steps *t* and *t+1* was calculated as 0.5 times the total occupancy of species *j* across all relevant states (in both habitats) at time step *t*. Extinction probabilities for both species were dependent on habitat type and whether the site was solely or jointly occupied. Species 1 was favored in habitat 1 and Species 2 was favored in habitat 2 and rates were symmetrical. Equilibrium conditions were identified by iterating forward from an even distribution of occupancy states within habitat, and the specified proportion of habitat type 1 (the habitat preferred by species 1).

Rcode with annotations in red

```
#below function iterates forward one time step a vector of the proportion of each of eight states
update<-function(p){# p is the proportion of sites in each of 8 possible sites and sums to 1
                    i1<-.5*(p[2]+p[4]+p[6]+p[8]) #colonization for species 1
```

```
        i2<-.5*(p[3]+p[4]+p[7]+p[8]) #colonization for species 2
        e1<-c(.1,.4) #extinction for species 1 when alone and in either habitat 1 or 2
        e12<-c(.2,1) #extinction for species 1 in presence of species 2 in habitat 1 or 2
        e2<-c(.4,.1) #extinction for species 2 when alone and in either habitat 1 or 2
        e21<-c(1,.2) #extinction for species 2 in presence of species 1 in habitat 1 or 2
        trans<-array(0,dim=c(8,8)) #transition matrix
        trans[1,1:4]<-c(1-(i2+i1-i2*i1),i1*(1-i2),i2*(1-i1),i2*i1)
        trans[2,1:4]<-c(e1[1]*(1-i2),(1-e1[1])*(1-i2),e1[1]*i2,(1-e1[1])*i2)
        trans[3,1:4]<-c(e2[1]*(1-i1),e2[1]*i1,(1-e2[1])*(1-i1),(1-e2[1])*i1)
        trans[4,1:4]<-c(e21[1]*e12[1],e21[1]*(1-e12[1]),e12[1]*(1-e21[1]),(1-e12[1])*(1-e21[1]))
        trans[5,5:8]<-c(1-(i2+i1-i2*i1),i1*(1-i2),i2*(1-i1),i2*i1)
        trans[6,5:8]<-c(e1[2]*(1-i2),(1-e1[2])*(1-i2),e1[2]*i2,(1-e1[2])*i2)
        trans[7,5:8]<-c(e2[2]*(1-i1),e2[2]*i1,(1-e2[2])*(1-i1),(1-e2[2])*i1)
        trans[8,5:8]<-c(e21[2]*e12[2],e21[2]*(1-e12[2]),e12[2]*(1-e21[2]),(1-e12[2])*(1-e21[2]))
        p%*%trans} #proportions after 1 time step
#This function iterates forward based on proportion of habitat type 1, h, to give final distribution of states. This function relies on update function above
habeq<-function(h){
    tt<-update(c(rep(h/4,4),rep((1-h)/4,4)))
    for (j in 1:10000){tt<-update2(tt)}
    sp1<- tt[2]+tt[4]+tt[6]+tt[8]
    sp2<- tt[3]+tt[4]+tt[7]+tt[8]
    return(c(sp1,sp2))}
data.eq<- matrix(NA,nrow=51,ncol=2) #array to hold equilibrium proportions for each species
for (h in 1:51){data.eq[h,]<-habeq(.01*(h-1))}
```

Figure A2 – Transient dynamics of invasion and competition based on estimates from barred owls and Northern spotted owls. Dynamics of invasion and competitive exclusion were simulated using parameter values based on estimates for barred owls and Northern spotted owls reported in Yackulic *et al.,* (2014). Whereas Yackulic *et al.,* (2014) used a logit link and considered variation between territories in colonization and extinction based on habitat, this analysis assumes colonization is linearly proportional to either regional or local occupancy and extinction only varies based on whether the conspecific is also present in the focal territory. By definition, each territory could be in one of four states (state 1: empty, state 2: barred owls only present, state 3: spotted owls only present, state 4:both species present). For both species at each time step, we first calculated the regional occupancy of that species (code below) or the occupancy over a local neighborhood of 100 territories. Next we multiplied these species specific regional or local neighborhood occupancies by species specific constants (for barred owls, i_b=0.7, and for spotted owls i_s=0.24) to derive time- and species-specific colonization rates. A transition matrix was then constructed using these values and the time-constant extinction values for barred owls alone (e_b=0.03), barred owls in territories also occupied by spotted owls (e_{bs}=0.1), spotted owls alone (e_s=0.08), and spotted owls in territories also occupied by barred owls (e_{sb}=0.27). This transition matrix was used to simulate forward stochastically one time step after which colonization was recalculated. Simulations ended when spotted owls were extirpated. Initial analyses suggested results were most sensitive to variation in e_{sb} and i_s. Increasing e_{sb} or decreasing i_s by 10% led to qualitatively similar results, including a ~25% decrease in the time to extinction when dispersal was regional and there were 200 territories in the region. Decreasing e_{sb} or increasing i_s by 10% led to qualitatively similar results as well.

Rcode for basic simulation function with annotations in red

```r
simmer<-function(N=200,Nyrs=500,nsims=100,ib=0.7,is=0.24,eb=0.03,ebs=0.1,es=0.08,esb=0.27){
    pbo.sum<-matrix(NA,ncol=Nyrs,nrow=nsims) # overall barred owl occupancy by year and simulation
    pso.sum<-matrix(NA,ncol=Nyrs,nrow=nsims) #same for spotted owls
    pbo.sum[j,1]<-0.05 #initial occupancy for barred owls
    pso.sum[j,1]<-0.5 #initial occupancy for spotted owls
    sbo<-ceiling(N*.05) #converted to number of territories
    sso<-ceiling(N*.5)
    for (j in 1:nsims){
        p<-rep(NA,N) #state of all territories in year 1
        p[1:sbo]<-2 # territories with barred owls
        p[(sbo+1):(sbo+sso)]<-3 # territories with spotted owls
        p[(sbo+sso+1):N]<-1 #empty territories
        for (k in 2:Nyrs){
            cb<-ib*sum(ifelse(p==2|p==4,1,0))/N #barred owl colonization rate
            cs<-is*sum(ifelse(p==3|p==4,1,0))/N #spotted owl colonization rate
            trans<-matrix(NA,ncol=4,nrow=4) #transition matrix
            trans[1,]<-c(1-(cs+cb-cs*cb),cb*(1-cs),cs*(1-cb),cs*cb)
            trans[2,]<-c(eb*(1-cs),(1-eb)*(1-cs),eb*cs,(1-eb)*cs)
            trans[3,]<-c(es*(1-cb),es*cb,(1-es)*(1-cb),(1-es)*cb)
            trans[4,]<-c(esb*ebs,esb*(1-ebs),ebs*(1-esb),(1-ebs)*(1-esb))
            for (i in 1:N){ #simulate changes in the state of individual territories
                p[i]<-sum(c(1:4)*rmultinom(1,1,trans[p[i],]))} #new state of all territories
            pbo.sum[j,k]<-sum(ifelse(p==2|p==4,1,0))/N # occupancy rate of barred owls
            pso.sum[j,k]<-sum(ifelse(p==3|p==4,1,0))/N # occupancy rate of spotted owls
            if (pso.sum[j,k]==0) (break)} #stop once spotted owls are extirpated
        }
    return(list(pbo.sum=pbo.sum,pso.sum=pso.sum))}
```