Notes for cue vs uptake vs half-saturation trade-off invasion model

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Contents

Set up

```
library(assertthat)
library(reshape2)
library(ggplot2)
library(GGally)
library(plyr)
library(rootSolve)
library(deSolve)
library(knitr)
library(pander)
library(cowplot)

#sourceFiles <- 'R/invasion.R'
#l_ply(sourceFiles, source)

set.seed(100) #reproducible random selection

sessionInfo()
```

```
## R version 3.3.2 (2016-10-31)
## Platform: x86_64-apple-darwin13.4.0 (64-bit)
## Running under: OS X Yosemite 10.10.5
##
## locale:
## [1] en_US.UTF-8/en_US.UTF-8/en_US.UTF-8/C/en_US.UTF-8/en_US.UTF-8
##
## attached base packages:
## [1] stats     graphics  grDevices utils     datasets  methods   base
##
## other attached packages:
##  [1] cowplot_0.7.0  pander_0.6.0   knitr_1.15.1   deSolve_1.14
##  [5] rootSolve_1.7  plyr_1.8.4     GGally_1.3.0   ggplot2_2.2.0
##  [9] reshape2_1.4.2 assertthat_0.1
##
## loaded via a namespace (and not attached):
##  [1] Rcpp_0.12.8        magrittr_1.5       munsell_0.4.3
##  [4] colorspace_1.3-1   stringr_1.1.0      tools_3.3.2
##  [7] grid_3.3.2         gtable_0.2.0       htmltools_0.3.5
## [10] yaml_2.1.14        lazyeval_0.2.0     rprojroot_1.1
## [13] digest_0.6.10      tibble_1.2         RColorBrewer_1.1-2
## [16] evaluate_0.10      rmarkdown_1.2      stringi_1.1.2
## [19] scales_0.4.1       backports_1.0.4    reshape_0.8.6
```

Basic model description

The goal of this model to simulation biologically mediated decomposition. There are two main pools, Substrate (C) and Biomass (B). Carbon is added to the substrate pool via inputs (I), leached from both pools at a rate proportional to the carbon in the pool (h fraction of the biomass pool B, and m fraction of the substate pool C), and transfer between the substrate C pool and biomass B pool via a Monod uptake with a maximum rate v_{max}, half-saturation constant k, and carbon use effiency ϵ_{cue}.

$\frac{dB}{dt} = \frac{\epsilon_{cue} v BC}{k+C} - hB$

$\frac{dC}{dt} = I - mC - \frac{vBC}{k+C}$

At steady state ($\frac{dB}{dt} = \frac{dC}{dt} = 0$) this implies that:

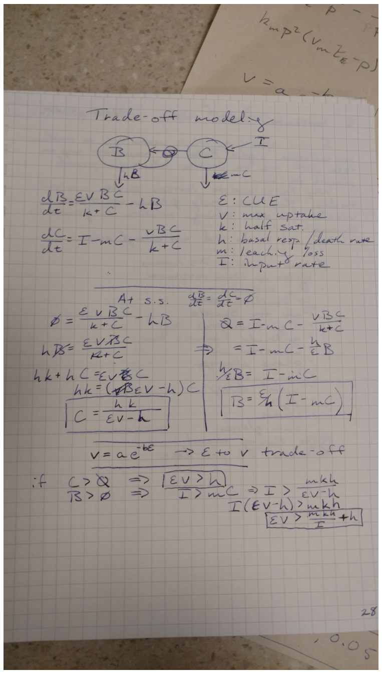
$B = \frac{\epsilon h}{I-mC}$

$C = \frac{hk}{\epsilon v - h}$

Calculate the leaching and turnover rate

Assume that the input rate, biomass, and carbon pools are given targets, and that we are exploring cue, v, and k. We can thus define the leaching and turnover rates at steady state:

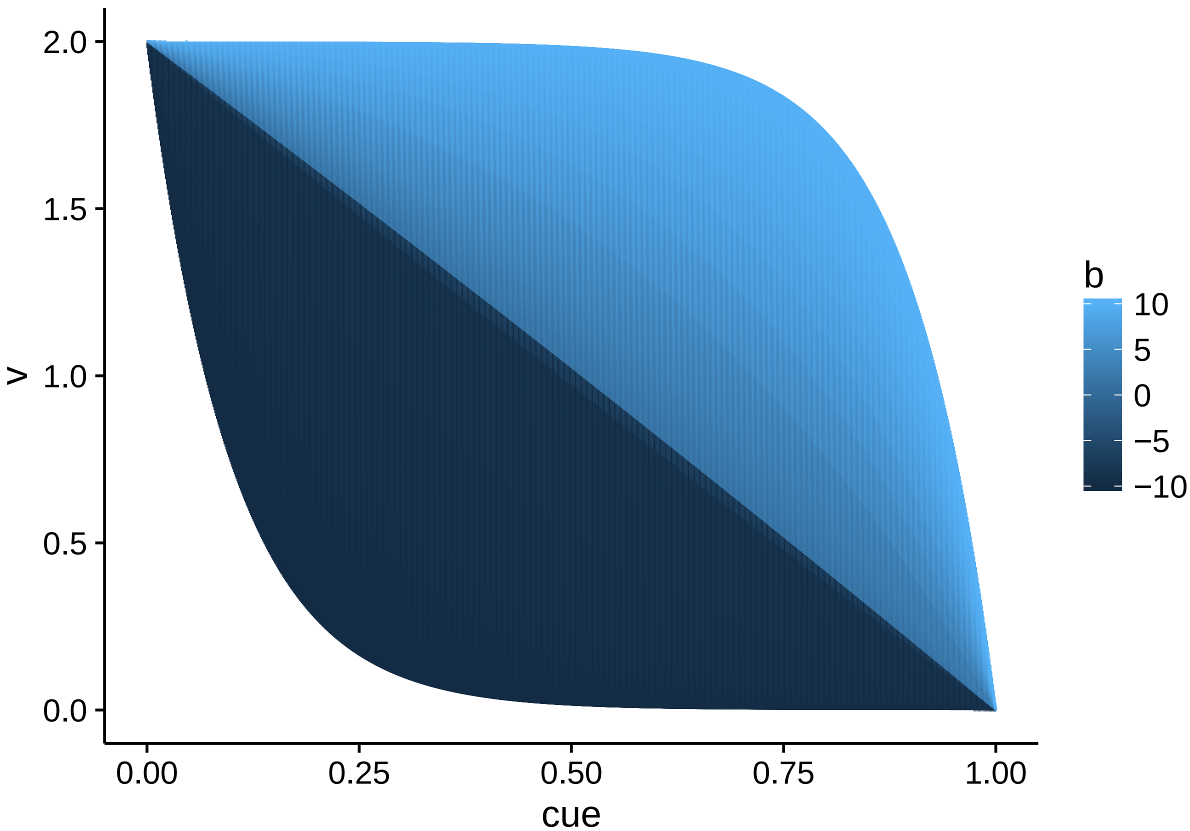
```r
find_h <- function(C, cue, v, k){
  return(C*cue*v/(k+C))
}

find_m <- function(cue, v, h, k, I, B){
  return((cue*v-h)/(cue*k)*(cue/h*I-B))
}
```



If we further assume that there is a trade off between both 1) uptake v and carbon use effiency (ϵ) such that $v = \frac{e^{b\epsilon_c ue} - e^b}{1-e^b}$ and the half saturation constant (k) such that $k = av + k_{min} = \frac{a}{1-e^b}(e^{b\epsilon_c ue} - e^b)$. Defined as:

Visualize trade-off between cue vs uptake and k

```
cue_v_tradeoff <- function(b, vmax, cue){
  return(vmax*(exp(b*cue)-exp(b))/(exp(0)-exp(b)))
}

tradeoff.df <- adply(.data=c(-0.1*1:9, -1*1:10, 0.1*1:9, 1:10), .margins=c(1), .id=c('id'), .fun=functi
  ans <- data.frame(b=b, cue=seq(0, 1, length=1000))
  ans$v <- cue_v_tradeoff(b=b, vmax=2, cue=ans$cue)
  return(ans)
})

ggplot(tradeoff.df) + geom_line(aes(x=cue, y=v, color=b))
```




```
v_k_tradeoff <- function(kmin, k_v_slope, v){
  return(kmin+k_v_slope*v)
}

tradeoff.df$k <- v_k_tradeoff(kmin=0, k_v_slope=100/2, tradeoff.df$v) #slope is max SOC over vmax range
```

This leads to the following steady state calculations for one biomass pool:

```
steadyState <- function(b, vmax, kmin, k_v_slope, h, m, I, cue){
  v <- cue_v_tradeoff(b=b, vmax=vmax, cue)
  k <- v_k_tradeoff(kmin=kmin, k_v_slope=k_v_slope, v=v)

  C <- h*k/(cue*v-h)
  B <- cue/h*(I-m*C)
  return(list(B=B, C=C))
}
```

Optimum carbon use effiency

We want the optimum carbon use effiency where biomass is maximum as steady state but that is not possible to solve analytically (you end up with $y = xe^x$, solve for x).

```
optimum_cue <- function(b, vmax, kmin, k_v_slope, h, m, I){
  cue <- seq(0, 1, length=100)
  ans <- steadyState(b, vmax, kmin, k_v_slope, h, m, I, cue)
```

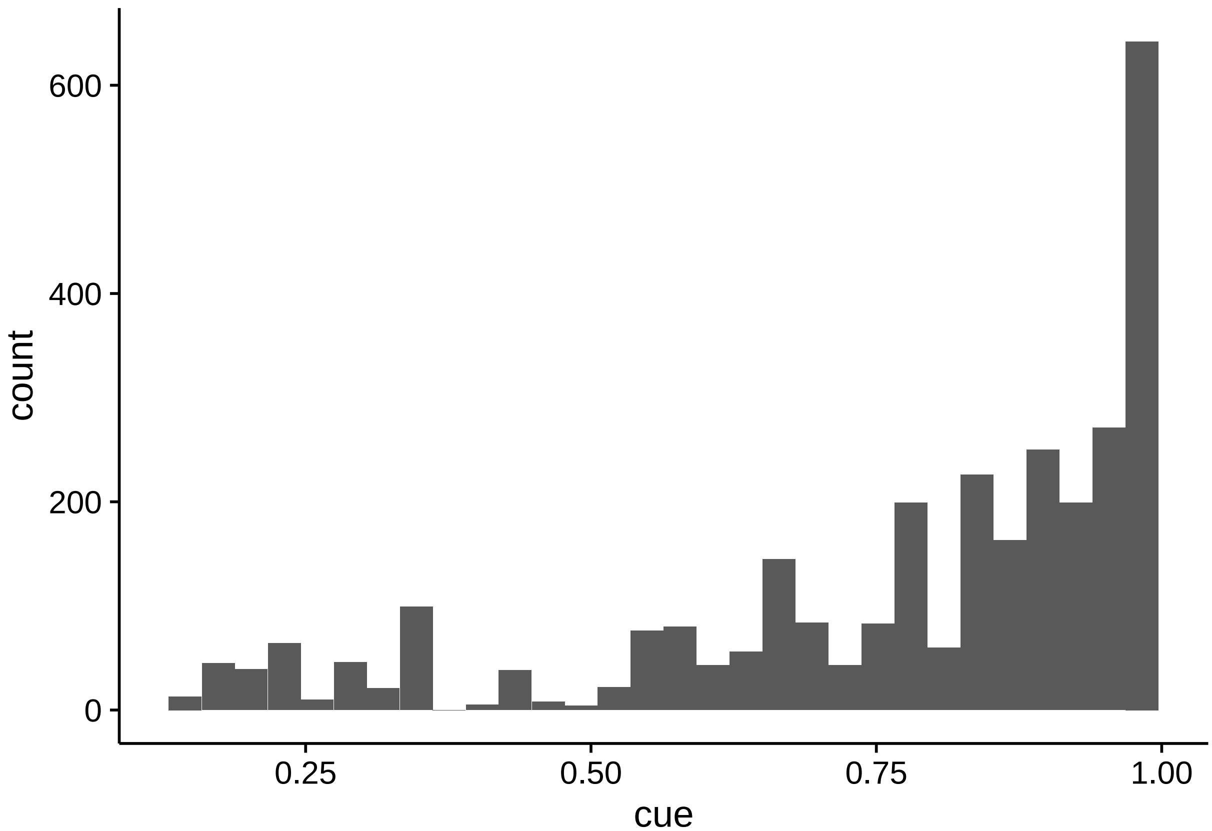
```
  ans$B[ans$B <= 0 | ans$C <= 0] <- -Inf

  best <- which.max(ans$B)
  return(list(B=ans$B[best], C=ans$C[best], cue=cue[best]))
}
```

Generate reasonable parameter sets without compitition

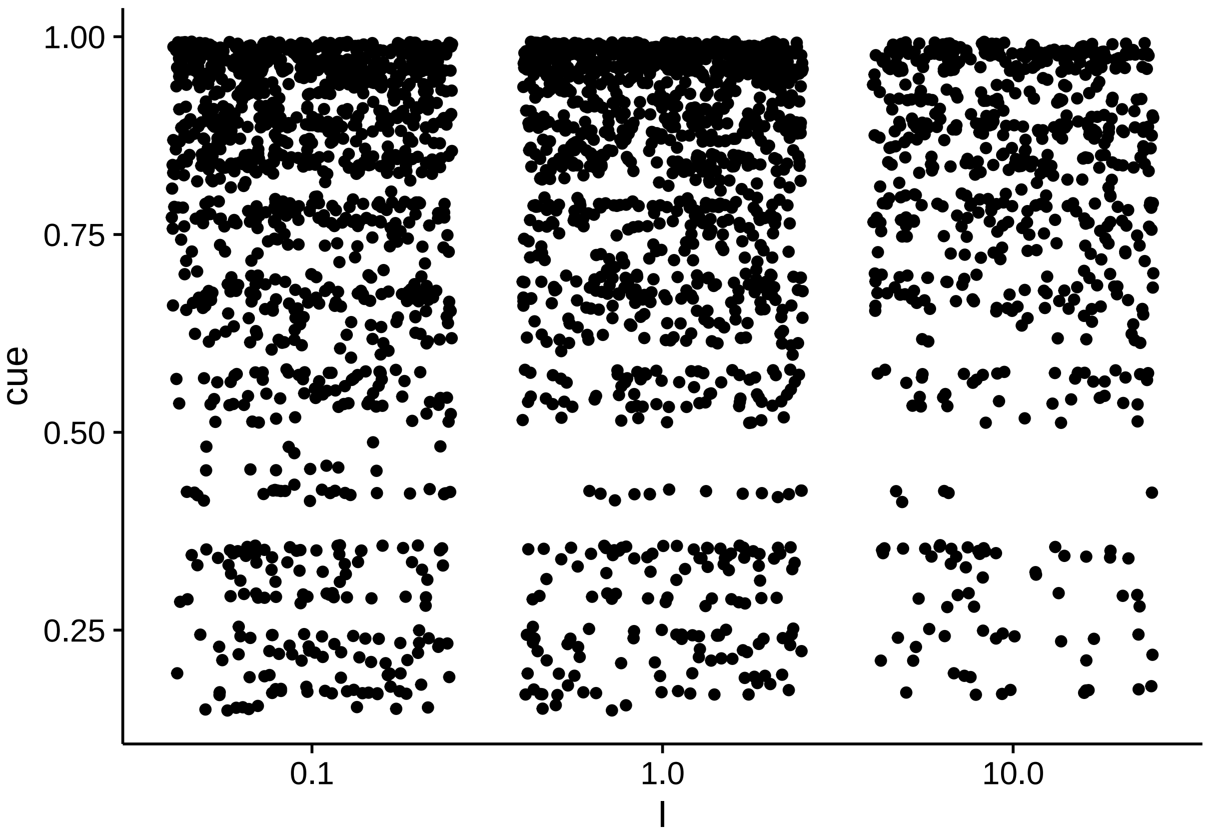
Given that we have input targets between 0.1 and 10 mg-C per g-soil per day, total carbon pools of between 10 to 500 mg-C per g-soil, and a biomass to total carbon ratio of between 0.1 and 15 percent. Let's generate some reasonable parameters to draw on.

```
parm.ls <- list(b=c(-10, -1, -0.1, 0.1, 1, 10),
                vmax=c(0.1, 0.5, 1, 5, 10, 100),
                kmin=c(0, 1, 10, 100, 1000),
                k_v_slope=c(1/10, 1, 10, 100, 1000),
                h=c(1e-4, 1e-3, 1e-2, 0.1, 1, 10),
                m=c(1e-4, 1e-3, 1e-2, 0.1, 1, 10),
                I=c(0.1, 1, 10))

optParm.df <- expand.grid(parm.ls)

optParm.df <- ddply(optParm.df, names(optParm.df), function(xx){
  ans <- as.data.frame(optimum_cue(b=xx$b, vmax=xx$vmax, kmin=xx$kmin, k_v_slope=xx$k_v_slope,
              h=xx$h, m=xx$m, I=xx$I))
  return(ans)
})

optParm.df$OnTarget <- with(optParm.df, B+C > 10 & B+C < 500 & B/(B+C)> 0.001 & B/(B+C) < 0.15)

#parm.allI <- ddply(subset(optParm.df, OnTarget), setdiff(names(parm.ls), 'I'), summarize,
#                  numI=length(I), minI=min(I), maxI=max(I))
#ggpairs(subset(optParm.df[,c(names(parm.ls), 'OnTarget')])

ggplot(subset(optParm.df, OnTarget)) + geom_histogram(aes(x=cue))
```

```
## `stat_bin()` using `bins = 30`. Pick better value with `binwidth`.
```



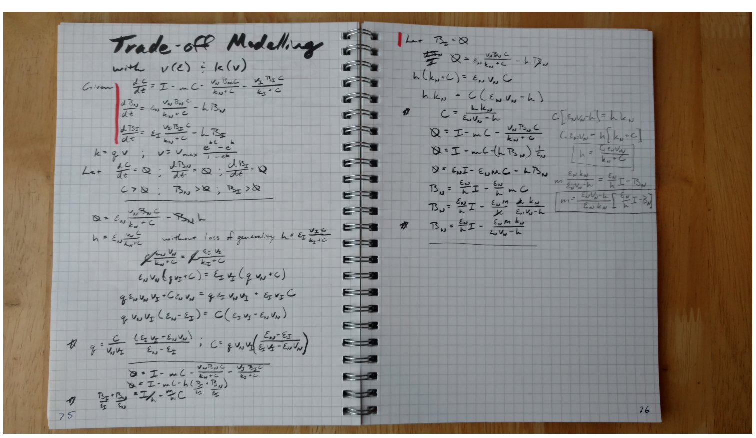

```
ggplot(subset(optParm.df, OnTarget)) + geom_jitter(aes(x=I, y=cue)) + scale_x_log10()
```




```
#ggplot(subset(optParm.df, OnTarget)) + geom_jitter(aes(x=I, y=B+C)) + scale_x_log10()
```

Competition model co-existance

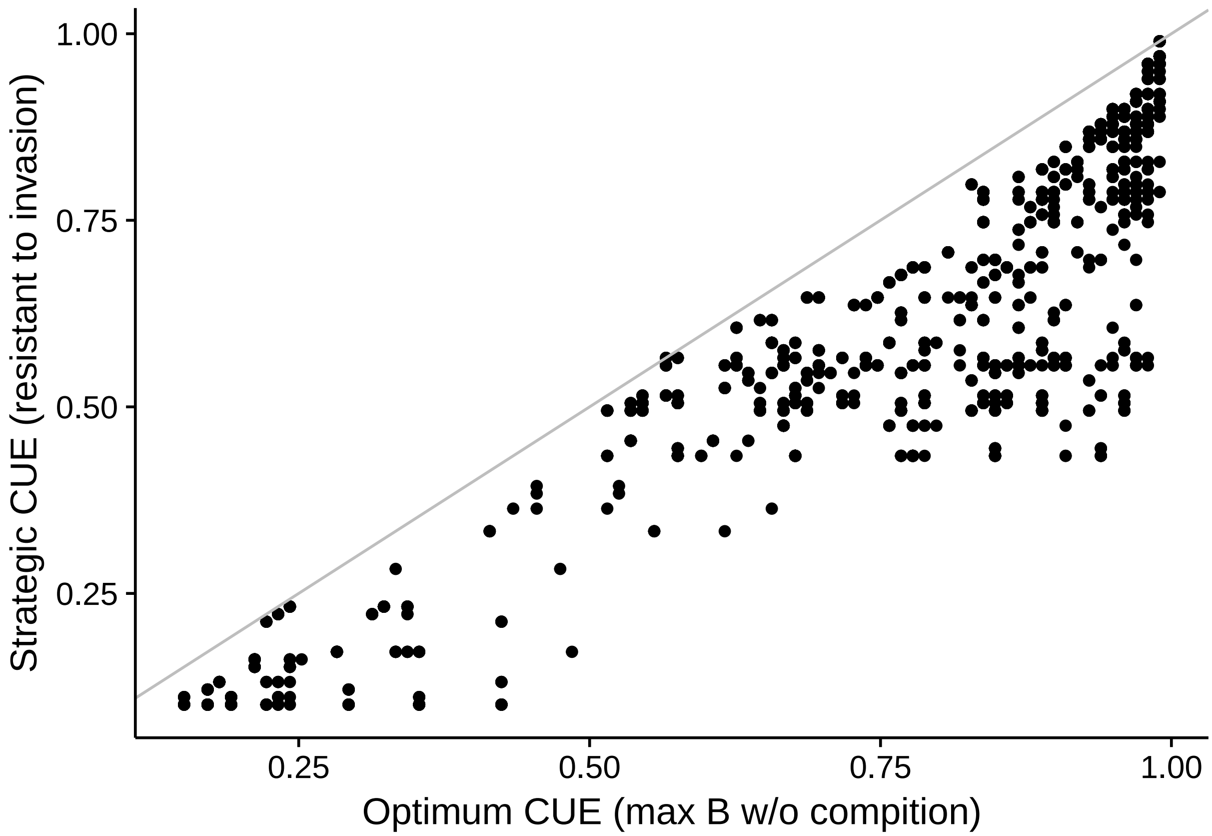
Consider the senerio where the native popuation is invated by a second competiting population that has a different carbon use effiency but is otherwise equivalent. Let the strategic carbon use effiency be where the native popuation is never invadable no matter what carbon use effiency value the invader has.



In otherwords both popuations are stable where one is either 0 or $\frac{\epsilon_n v_n}{k_n+C} = \frac{\epsilon_i v_i}{k_i+C}$ where n and i stand for the native and invading populations respectively.

Again, not solvable analytically given our trade-off function but numerically we can calculate the following:

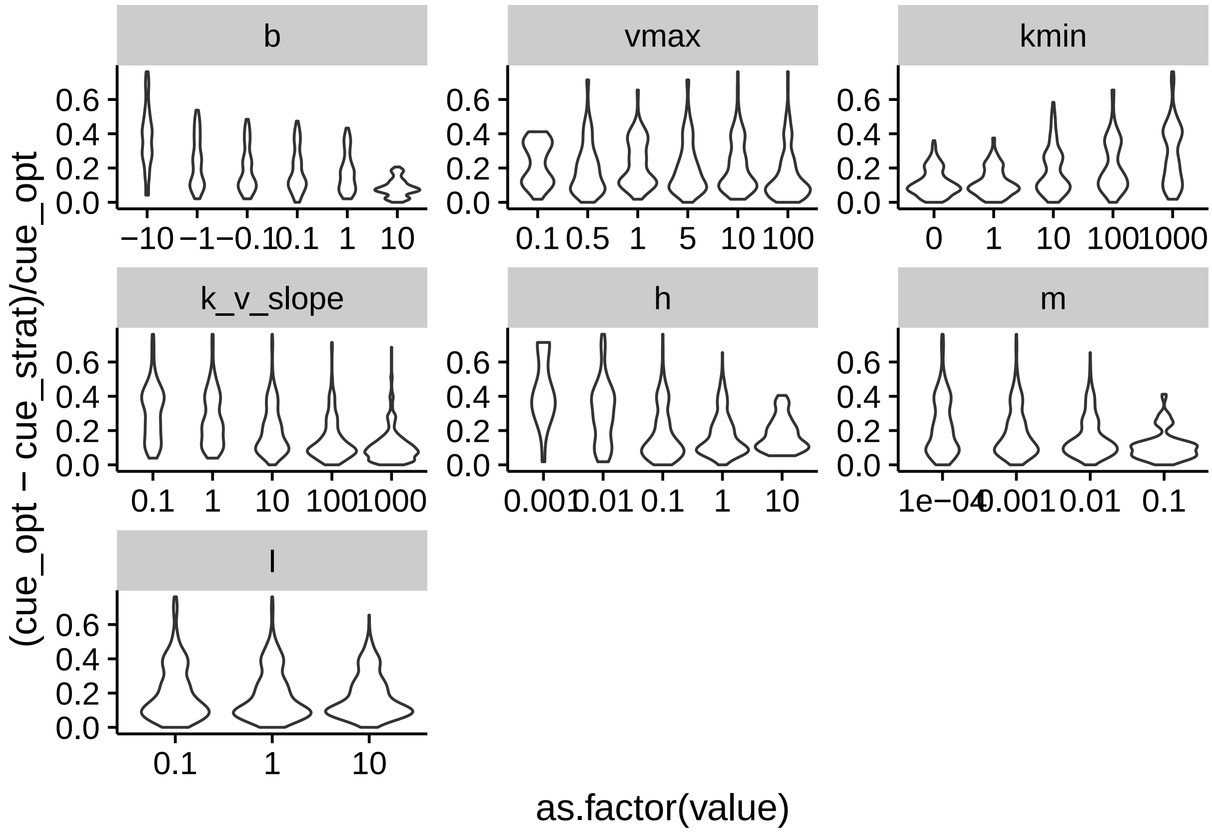
```r
strategic_cueI <- function(b, vmax, kmin, k_v_slope, m, h, I){
  cue <- seq(0, 1, length=100)
  v <- cue_v_tradeoff(b=b, vmax=vmax, cue)
  k <- v_k_tradeoff(kmin=kmin, k_v_slope=k_v_slope, v=v)

  ans <- steadyState(b, vmax, kmin, k_v_slope, h, m, I, cue)

  measure <- cue*v/(k+ans$C)
  measure[measure <= 0] <- NA
  flag <- which.max(measure)

  return(list(cue_strat=cue[flag], C_strat=ans$C[flag], B_strat=ans$B[flag]))
}

stratParm.df <- optParm.df
stratParm.df <- rename(stratParm.df, c('cue'='cue_opt', 'B'='B_opt', 'C'='C_opt', 'OnTarget'='validPools
stratParm.df <- ddply(stratParm.df, names(stratParm.df), function(xx){
  return(as.data.frame(strategic_cueI(b=xx$b, vmax=xx$vmax, kmin=xx$kmin,
                        k_v_slope=xx$k_v_slope, m=xx$m, h=xx$h, I=xx$I)))
})

stratParm.df$validPools_strat <- with(stratParm.df, B_strat+C_strat > 10 &
                                        B_strat+C_strat < 500 &
                                        B_strat/(B_strat+C_strat)> 0.001 &
                                        B_strat/(B_strat+C_strat) < 0.15)
stratParm.df$orderDiff_mh <- round(log(stratParm.df$m)-log(stratParm.df$h), 1)
ggplot(subset(stratParm.df, validPools_opt & validPools_strat)) +
  geom_point(aes(x=cue_opt, y=cue_strat)) +
  geom_abline(slope=1, intercept=c(0), color='grey') +
  labs(x='Optimum CUE (max B w/o compition)', y='Strategic CUE (resistant to invasion)')
```




```
#test.parm <- as.list(stratParm.df[1,])
#attach(test.parm)
#detach(test.parm)
```

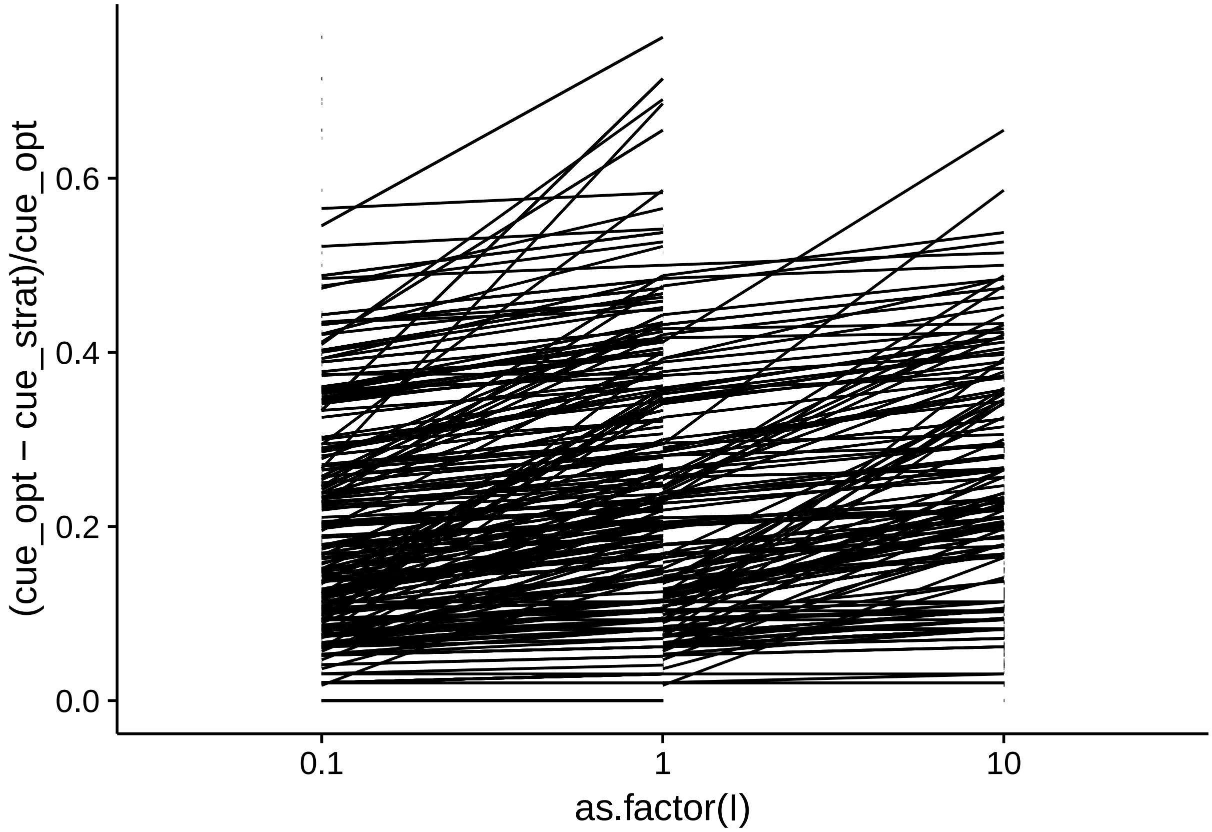
Explore drivers of strategic and optimum differences

```
diff.df <- subset(stratParm.df, validPools_opt & validPools_strat,
                  select=setdiff(names(stratParm.df), c('orderDiff_mh')))

diff.df <- melt(diff.df, measure.vars=names(parm.ls))

ggplot(diff.df) + geom_violin(aes(x=as.factor(value), y=(cue_opt-cue_strat)/cue_opt)) +
    facet_wrap(~variable, scale='free')
```

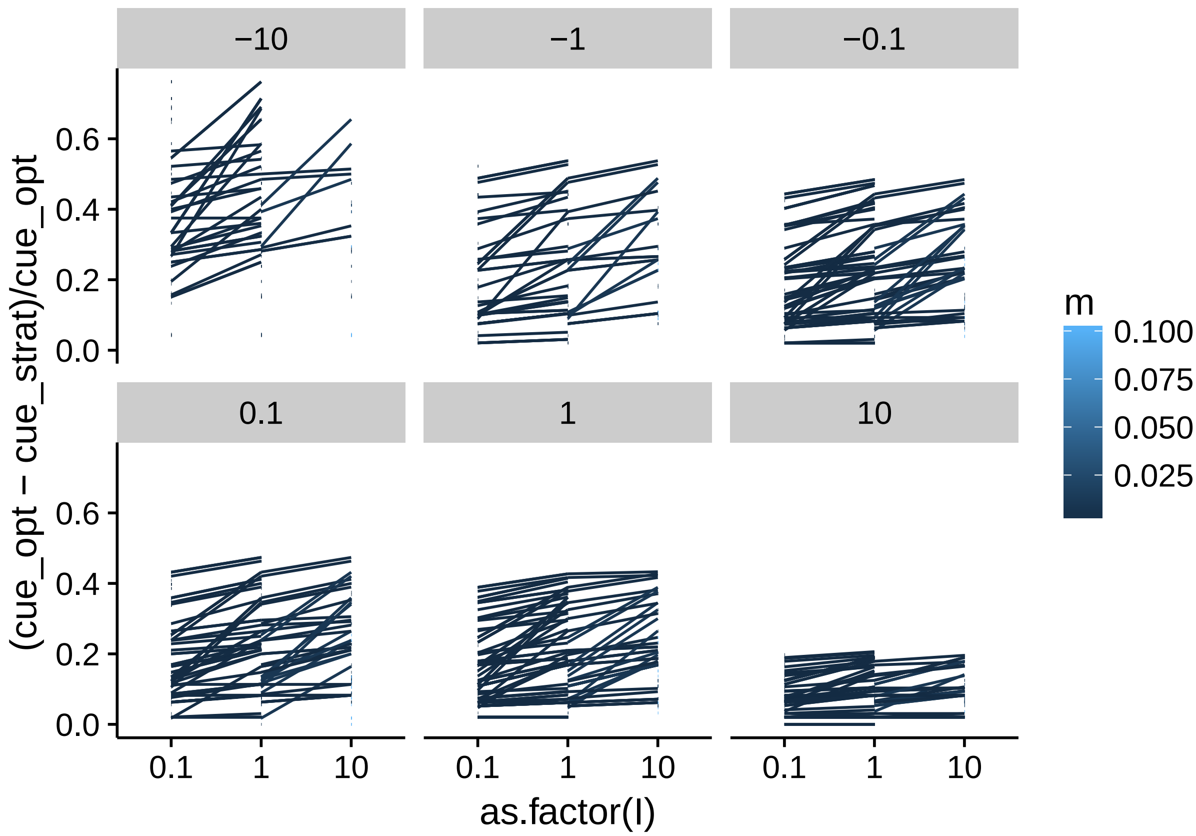


We are particullary interested in differences in inputs

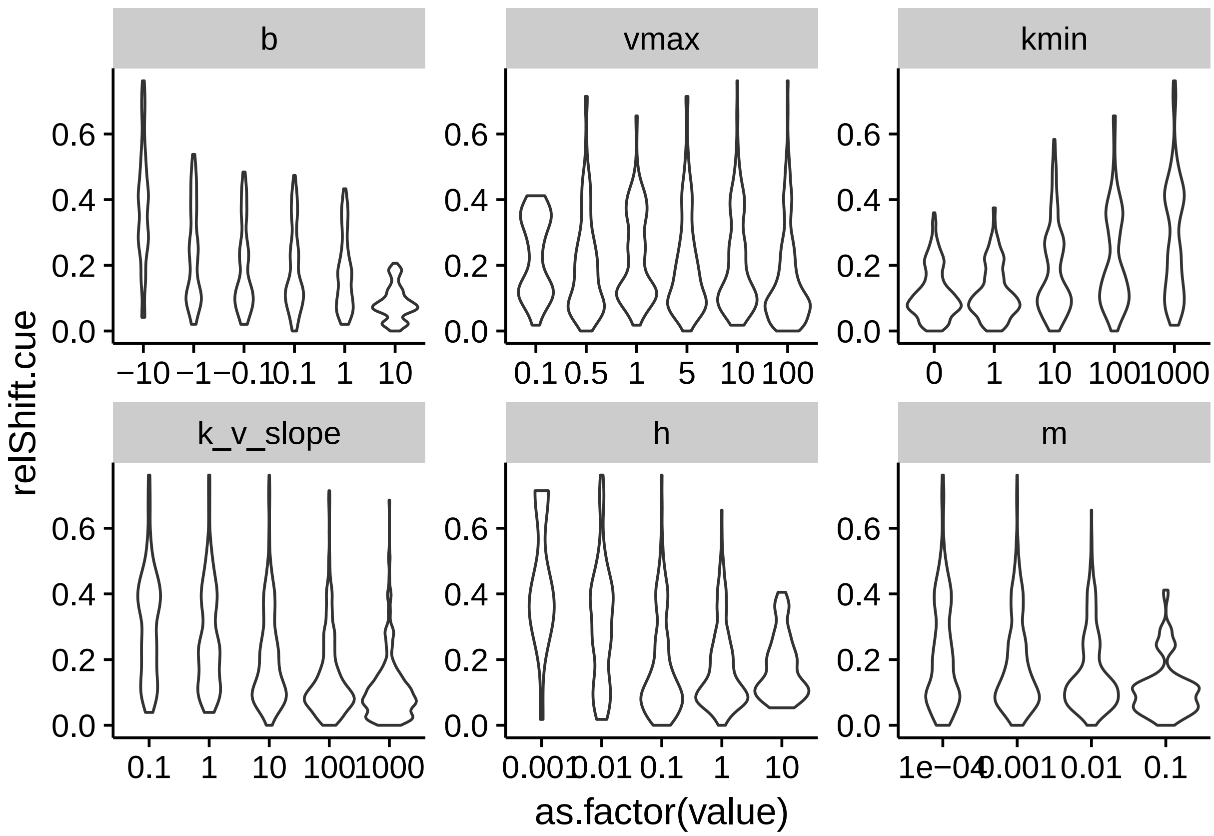
```
inputIndex <- unique(stratParm.df[, setdiff(names(parm.ls), 'I')])
inputIndex$nonI.index <- 1:nrow(inputIndex)

inputIndex <- merge(stratParm.df, inputIndex)
range <- ddply(subset(inputIndex, validPools_opt & validPools_strat), c('nonI.index'), summarize,
                    relShift.cue=range((cue_opt-cue_strat)/cue_opt, na.rm=TRUE))

inputIndex <- merge(inputIndex, range)
inputIndex <- subset(inputIndex, validPools_opt & validPools_strat)
ggplot(inputIndex) + geom_line(aes(x=as.factor(I), y=(cue_opt-cue_strat)/cue_opt, group=nonI.index))
```




```
ggplot(inputIndex) + geom_line(aes(x=as.factor(I), y=(cue_opt-cue_strat)/cue_opt, group=nonI.index, colo
```




```
plot.df <- melt(inputIndex, measure.vars=setdiff(names(parm.ls), 'I'))
ggplot(plot.df) + geom_violin(aes(x=as.factor(value), y=relShift.cue)) + facet_wrap(~variable, scales='
```



Numerical validation code

Let's pick some points where the gap between the Optimum CUE and Strategic CUE is small (< 20 percent) and large (> 20 percent).

```
bigGap.df <- subset(stratParm.df, validPools_opt & validPools_strat & abs(cue_strat-cue_opt) > 0.2)
smallGap.df <- subset(stratParm.df, validPools_opt & validPools_strat & abs(cue_strat-cue_opt) < 0.2)

numParm.df <- rbind.fill(bigGap.df[sample.int(nrow(bigGap.df), size=2),],
                         smallGap.df[sample.int(nrow(smallGap.df), size=2),])
numParm.df$index <- 1:nrow(numParm.df)
pander(numParm.df[,c(names(parm.ls), c('cue_opt','C_opt', 'B_opt', 'cue_strat','C_strat', 'B_strat'))])
```

Table 1: Table continues below

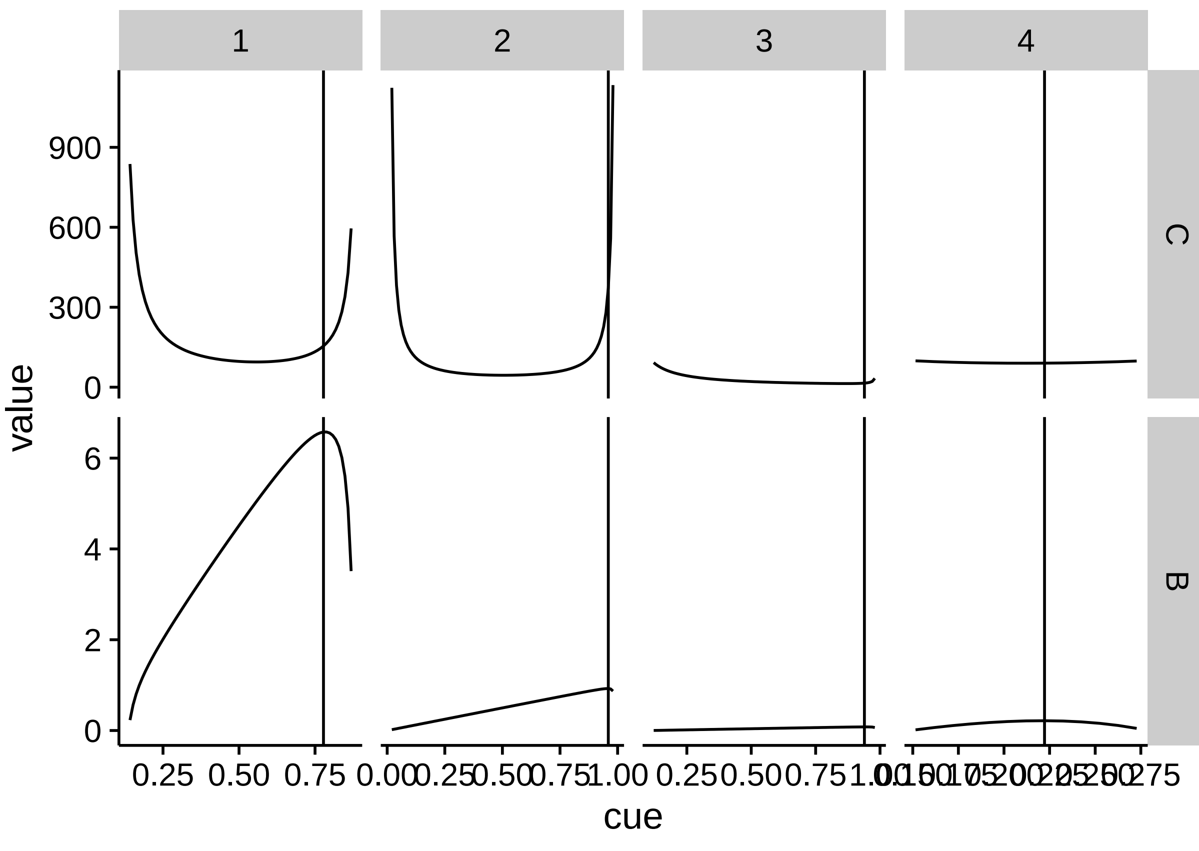
b	vmax	kmin	k_v_slope	h	m	I	cue_opt	C_opt	B_opt
0.1	0.1	100	1000	0.01	1e-04	0.1	0.7778	154.6	6.575
-0.1	100	1000	1	1	1e-04	1	0.9596	372.6	0.9238
-0.1	100	10	10	1	0.001	0.1	0.9394	15.31	0.07956
-10	10	1000	1000	0.01	0.001	0.1	0.2222	90.29	0.2157

cue_strat	C_strat	B_strat
0.5556	94.73	5.029

cue_strat	C_strat	B_strat
0.5051	44.86	0.5028
0.8687	13.68	0.07498
0.2121	90.02	0.2117

Validate optimium CUE

```
opt.validate <- ddply(numParm.df, c('index', 'C_opt', 'B_opt'), function(xx){
  cue <- seq(0, 1, length=100)
  ans <- steadyState(xx$b, xx$vmax, xx$kmin, xx$k_v_slope, xx$h, xx$m, xx$I, cue)
  return(data.frame(cue=cue, C=ans$C, B=ans$B))
})

plot.df <- melt(subset(opt.validate, B>0 & C>0), measure.vars=c('C', 'B'))
ggplot(plot.df) + geom_line(aes(x=cue, y=value, group=index)) +
  geom_vline(data=numParm.df, aes(xintercept=cue_opt)) +
  facet_grid(variable~index, scales='free')
```

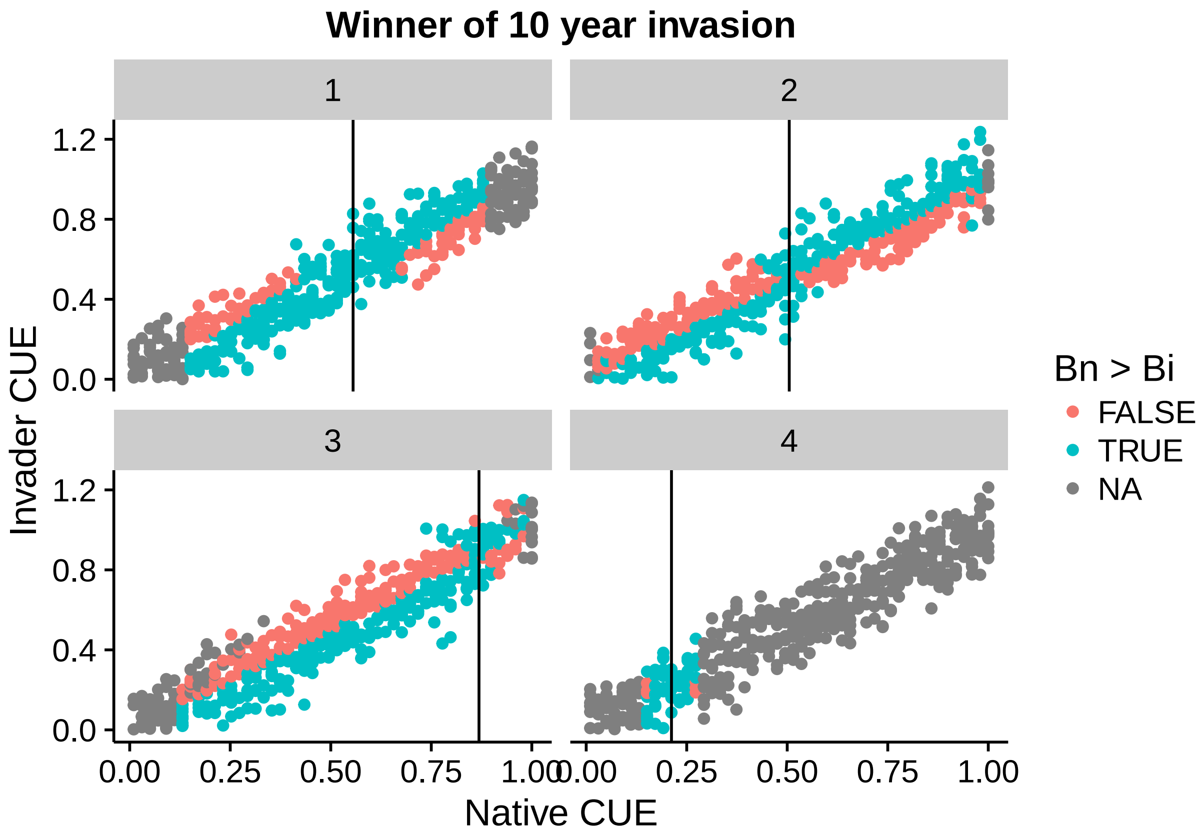


Validate strategic CUE

```
compitition.model <- function(t, y, parms){
  C <- y[1]; Bn <- y[2]; Bi <- y[3]
```

```
  ans <- with(parms,
              c(dC = I - m*C - C*(vn*Bn/(kn+C) + vi*Bi/(ki+C)),
                   dBn = cuen*vn*Bn*C/(kn+C) - hn*Bn,
                   dBi = cuei*vi*Bi*C/(ki+C) - hi*Bi)
       )
  return(list(ans))
}

runInvasions <- ddply(numParm.df, c('index'), function(xx){

  parm <- as.list(xx[, c('b', 'vmax', 'kmin', 'k_v_slope', 'm', 'I')])

  parm$hn <- xx$h
  parm$hi <- xx$h

  cueCombo <- expand.grid(cuen=seq(1, 100, length=50)/100,
                          rel_cuei=rnorm(10, sd=0.1))
  cueCombo$cuei <- cueCombo$cuen+rnorm(nrow(cueCombo), sd=0.1)
  cueCombo <- cueCombo[cueCombo$cuei > 0,]

  cueCombo$vn <- with(parm, cue_v_tradeoff(b=b, vmax=vmax, cueCombo$cuen))
  cueCombo$kn <- with(parm, v_k_tradeoff(kmin=kmin, k_v_slope=k_v_slope, v=cueCombo$vn))

  cueCombo$vi <- with(parm, cue_v_tradeoff(b=b, vmax=vmax, cueCombo$cuei))
  cueCombo$ki <- with(parm, v_k_tradeoff(kmin=kmin, k_v_slope=k_v_slope, v=cueCombo$vi))

  invade.df <- ddply(cueCombo, c('cuen', 'cuei'), function(cuePairs){
    comboParm <- c(parm, cuePairs)
    preInvade <- with(comboParm, steadyState(b, vmax, kmin, k_v_slope, h=hn, m, I, cue=cuen))
    if(all(preInvade > 0)){
      y0 <- list(C=preInvade$C, Bn=preInvade$B, Bi=preInvade$B*0.1)
      invasion <- lsoda(y=unlist(y0), times=c(1, 7, 30, 365, 365*10), func=compitition.model, parms=comb
      names(y0) <- paste(names(y0), '0', sep='')
      if(nrow(invasion) == 5){
        finalPools <- as.data.frame(c(comboParm, y0, as.list(invasion[nrow(invasion),])))
      }else{
        finalPools <- as.data.frame(comboParm)
      }
    }else{
      finalPools <- as.data.frame(comboParm)
    }
  })

  return(invade.df)
})
```

```
ggplot(runInvasions) + geom_point(aes(x=cuen, y=cuei, color=Bn > Bi)) +
  geom_vline(data=numParm.df, aes(xintercept=cue_strat)) +
  labs(x='Native CUE', y='Invader CUE', title='Winner of 10 year invasion') +
  facet_wrap(~index)
```



Winner of 10 year invasion
1
2
3
4
1.2
0.8
0.4
0.0
Invader CUE
0.00
0.25
0.50
0.75
1.00
Native CUE
Bn > Bi
FALSE
TRUE
NA