Appendix S2. Evolutionary drivers of species and community dynamics

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1 Background

In Appendix S1.5, we evaluated the ability of the statistical model to estimate the impact of trait evolution for species abundances. Trait evolution's impact for species abundances can be modeled as a predictor in different ways. Here we derive the numerical form of the trait x_i that we hypothesize has the most impact on species abundances.

2 Model for population growth, competition, environmental change, and evolution

The growth equation for each species is:

$$N_{i,t+1} = \frac{\hat{W} e^{\frac{-[(\frac{w+(1-h^2)P}{P+w})(E-x_{i,t})]^2}{2(P+w)}} N_{i,t}}{1+\alpha_{ii}N_{i,t}+\alpha_{ij}N_{j,t}}$$

We simulate population growth under particular parameter values, to generate population dynamics where species interactions, environment, and trait evolution all drive population dynamics.

```
# Case 1: Weaker interactions, stronger environment
# Simulate initial species population growth with environment fluctuations
N1.0 <- 10
N2.0 <- 10
alpha.11 <- 0.01
alpha.22 <- 0.01
alpha.12 <- 0.005
alpha.21 <- 0.01
E.0 <- 0.8
x1.0 <- 0.6
x2.0 <- 0.8
P <- 1
w <- 10
```

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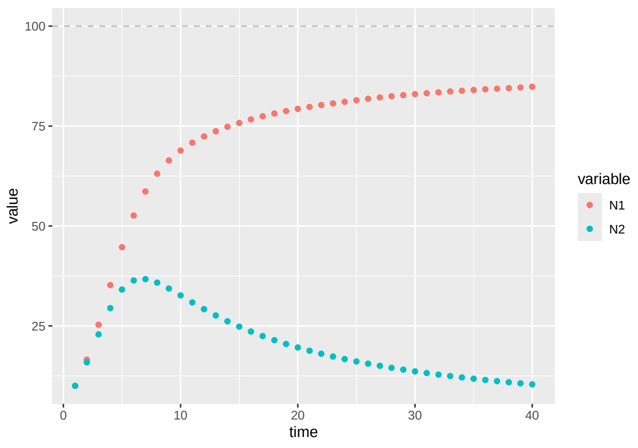
```
Wmax <- 2
h2 <- 0.1
k <- (w+(1-h2)*P)/(P+w)

# model function
disc_LV_evol <- function(N1.0,N2.0,alpha.11,alpha.22,alpha.12,alpha.21,E,x1.0,x2.0,P,w,Wmax,h2) {
  What <- Wmax*sqrt(w/(P+w))
  r1 <- What*exp((-(((w+(1-h2)*P)/(P+w))*(E-x1.0))^2)/(2*(P+w)))
  Nt1 <- (r1*N1.0) / (1+alpha.11*N1.0+alpha.12*N2.0)
  r2 <- What*exp((-(((w+(1-h2)*P)/(P+w))*(E-x2.0))^2)/(2*(P+w)))
  Nt2 <- (r2*N2.0) / (1+alpha.22*N2.0+alpha.21*N1.0)
  return(c(Nt1,Nt2,r1,r2))
}
# Simulation of model for t time steps
t <- 40
N <- array(NA,dim=c(t,2))
N <- as.data.frame(N)
colnames(N) <- c("N1","N2")
x <- array(NA,dim=c(t,2))
x <- as.data.frame(x)
colnames(x) <- c("x1","x2")
r <- array(NA,dim=c(t,2))
r <- as.data.frame(r)
colnames(r) <- c("r1","r2")
N$N1[1] <- N1.0
N$N2[1] <- N2.0
x$x1[1] <- x1.0
x$x2[1] <- x2.0
r$r1[1] <- exp((-(((w+(1-h2)*P)/(P+w))*(E.0-x1.0))^2)/(2*(P+w)))
r$r2[1] <- exp((-(((w+(1-h2)*P)/(P+w))*(E.0-x2.0))^2)/(2*(P+w)))
E <- rep(NA, t)
E[1] <- E.0
for (i in 2:t) {
  res <- disc_LV_evol(N1.0=N[i-1,1],N2.0=N[i-1,2],alpha.11=alpha.11,alpha.22=alpha.22,alpha.12=alpha.12
  N$N1[i] <- res[1]
  N$N2[i] <- res[2]
  r$r1[i] <- res[3]
  r$r2[i] <- res[4]
  # trait change
  d1 <- E[i-1] - x[i-1,1]
  d2 <- E[i-1] - x[i-1,2]
  d1.1 <- k*d1
  d2.1 <- k*d2
  x$x1[i] <- E[i-1] - d1.1
  x$x2[i] <- E[i-1] - d2.1
  # environmental change
  E[i] <- E[i-1] + rnorm(1,0,.01)
}
```

```
# Plot simulation: ggplot
N$time <- 1:t
dat <- melt(N, id.vars="time")
ggplot2::ggplot(dat, aes(time, value, col=variable)) + geom_point() + geom_hline(yintercept = (1/alpha.
```

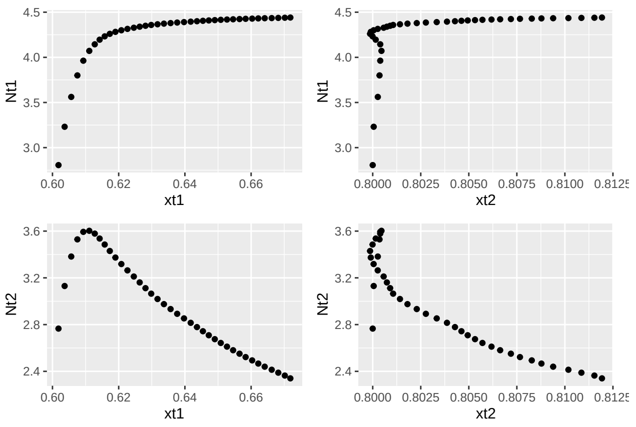


3 Hypotheses for evolution as a driver of species abundances

The growth equation is not linear, yet we fit abundance data to a heirarchical model with linear predictors because in most natural systems, a single theoretical growth model can't adequately capture the complexity in a given system. Linear models don't capture mechanistic relationships, but instead correlative. They are useful for inferring direction and magnitude of effect sizes. In Appendix S1, we explore how non-linear dynamics are captured when fit to a linear model. Here, we explore different forms to encode evolution in the trait x that determines the organism's fitness in this system.

3.1 H1. Raw trait value drives species abundances

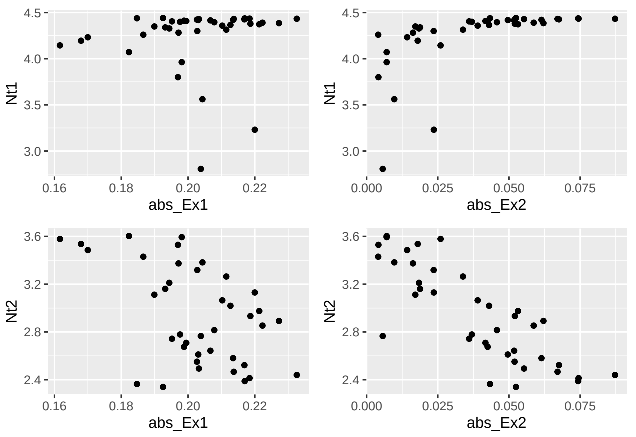
```
# Plot simulation: ggplot
dat <- as.data.frame(cbind(log(N$N1),log(N$N2),x$x1,x$x2))
colnames(dat) <- c("N1","N2","x1","x2")
dat$time <- 1:t
df <- data.frame(cbind(dat$N1[2:t],dat$N2[2:t],dat$x1[2:t],dat$x2[2:t]))
colnames(df) <- c("Nt1","Nt2","xt1","xt2")
# Plot
p1 <- ggplot2::ggplot(df, aes(xt1, Nt1)) + geom_point()
p2 <- ggplot2::ggplot(df, aes(xt2, Nt1)) + geom_point()
p3 <- ggplot2::ggplot(df, aes(xt1, Nt2)) + geom_point()
p4 <- ggplot2::ggplot(df, aes(xt2, Nt2)) + geom_point()
p1 + p2 + p3 + p4
```



We do not hypothesize that the raw trait value is the best predictor of species abundances, because the impacts of this evolved trait depend on the context of the environment.

3.2 H2. Absolute value of trait distance from optimum drives species abundances

```r
# Plot simulation: ggplot
df$E <- E[2:t]
df$abs_Ex1 <- abs(df$E - df$xt1)
df$abs_Ex2 <- abs(df$E - df$xt2)
# Plot
p1 <- ggplot2::ggplot(df, aes(abs_Ex1, Nt1)) + geom_point()
p2 <- ggplot2::ggplot(df, aes(abs_Ex2, Nt1)) + geom_point()
p3 <- ggplot2::ggplot(df, aes(abs_Ex1, Nt2)) + geom_point()
p4 <- ggplot2::ggplot(df, aes(abs_Ex2, Nt2)) + geom_point()
p1 + p2 + p3 + p4
```

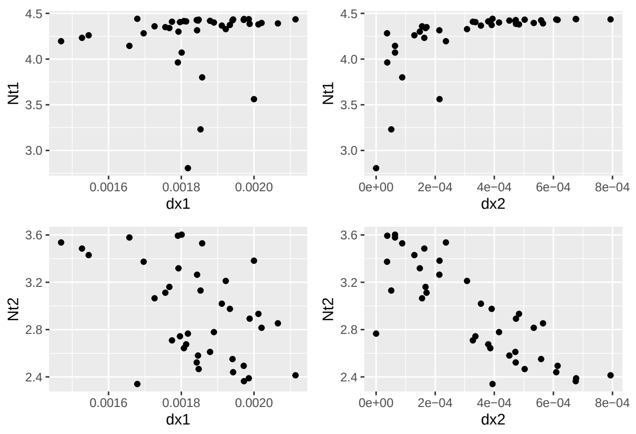


We hypothesize that this represents the true impact on species abundances, via the direct impact this measure has on fitness and consequent population growth. However, we also acknowledge this is likely difficult to measure in most empirical systems.

3.3 H3. Absolute value of trait change from one time to the next drives species abundances

We now onsider the magnitude of trait change from one time step to the next as a driver for species abundances.

```r
df$dx1 <- abs(dat$x1[2:t] - dat$x1[1:(t-1)])
df$dx2 <- abs(dat$x2[2:t] - dat$x2[1:(t-1)])
# Plot
p1 <- ggplot2::ggplot(df, aes(dx1, Nt1)) + geom_point()
p2 <- ggplot2::ggplot(df, aes(dx2, Nt1)) + geom_point()
p3 <- ggplot2::ggplot(df, aes(dx1, Nt2)) + geom_point()
p4 <- ggplot2::ggplot(df, aes(dx2, Nt2)) + geom_point()
p1 + p2 + p3 + p4
```

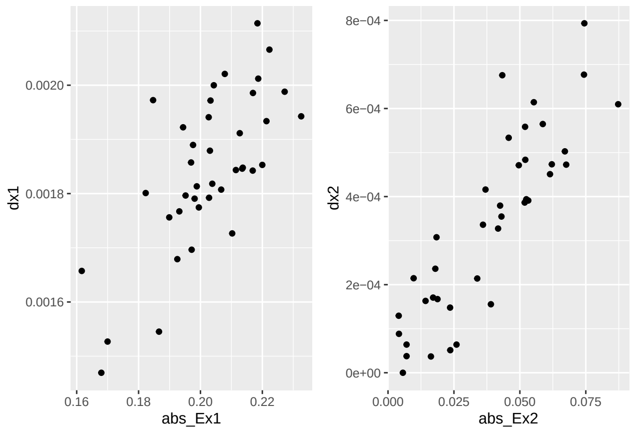


The measures correlate highly with one another, as the amount of trait change (the amount of evolution) is determined by the distance to the optimum trait value (given that P and w remain constant in the simulation).

```r
cor(df$dx1, df$abs_Ex1)
#> [1] 0.7104567
```

```r
cor(df$dx2, df$abs_Ex2)
#> [1] 0.8726185
```

```r
# Plot
p1 <- ggplot2::ggplot(df, aes(abs_Ex1,dx1)) + geom_point()
p2 <- ggplot2::ggplot(df, aes(abs_Ex2,dx2)) + geom_point()
p1 + p2
```



4 Statistical model for evolution as a driver of species abundances

We hypothesize that $|E_t - x_{i,t}|$ will be the best predictor of species abundances, and that $|x_{t+1} - x_{i,t}|$ will have similar explanatory power.

```
# prepare data in HMSC format
dat <- as.data.frame(cbind(log(N$N1),log(N$N2),x$x1,x$x2))
colnames(dat) <- c("N1","N2","x1","x2")
dat$time <- 1:t
df <- data.frame(cbind(dat$N1[2:t],dat$N2[2:t],dat$x1[2:t],dat$x2[2:t]))
colnames(df) <- c("Nt1","Nt2","xt1","xt2")
df$dx1 <- abs(dat$x1[2:t] - dat$x1[1:(t-1)])
df$dx2 <- abs(dat$x2[2:t] - dat$x2[1:(t-1)])
# Y matrix
Y <- as.matrix(cbind(df$Nt1,df$Nt2))
# X matrix
XData <- data.frame(cbind(dat$N1[1:(t-1)],dat$N2[1:(t-1)]),E[1:(t-1)],E[1:(t-1)]^2,dat$x1[1:(t-1)],dat$
colnames(XData) <- c("n1","n2","E","Esq","x1","x2","dx1","dx2","dEx1","dEx2")
# Prepare HMSC model
studyDesign = data.frame(sample = as.factor(1:(t-1)))
rL = HmscRandomLevel(units = studyDesign$sample)
# Design and fit 4 alternative HMSC models
models = list()
for(i in 1:4){
  XFormula = switch(i, ~1, ~E+Esq+x1+x2, ~E+Esq+dEx1+dEx2, ~E+Esq+dx1+dx2)
  m = Hmsc(Y = Y, XData = XData, XFormula = XFormula, studyDesign = studyDesign, ranLevels = list(sampl
  models[[i]] = m
}
# Bayesian model parameters
nChains <- 2
thin <- 5
samples <- 2000
transient <- 100*thin
verbose <- 500*thin
for(i in 1:4){
  models[[i]] = sampleMcmc(models[[i]],thin=thin,sample=samples,transient=transient,nChains=nChains,ver
}
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
#> Chain 1, iteration 5000 of 10500 (sampling)
#> Chain 1, iteration 7500 of 10500 (sampling)
#> Chain 1, iteration 10000 of 10500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
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#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
#> Chain 2, iteration 5000 of 10500 (sampling)
#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
```

We check the explanatory and predictive power of each model using cross-validation.

```r
# After Ovaskainen & Abrego 2020, Chapter 7
partition = createPartition(m,nfolds=2,column="sample")
partition.sp = c(1,2)
result = matrix(NA,nrow=3,ncol=4)
for(i in 1:4){
  m = models[[i]]
  # Explanatory power
  preds = computePredictedValues(m)
  MF = evaluateModelFit(hM=m,predY=preds)
  result[1,i] = mean(MF$R2)
  # Predictive power based on cross-validation
  preds = computePredictedValues(m,partition=partition)
  MF = evaluateModelFit(hM=m,predY=preds)
  result[2,i] <- mean(MF$R2)
  # Predictive power based on conditional cross-validation
  preds = computePredictedValues(m,partition=partition,partition.sp=partition.sp,mcmcStep=100)
  MF = evaluateModelFit(hM=m,predY=preds)
  result[3,i] = mean(MF$R2)
}
#> Cross-validation, fold 1 out of 2
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
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#> Cross-validation, fold 2 out of 2
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#> Cross-validation, fold 2 out of 2
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#> Cross-validation, fold 2 out of 2
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#> Cross-validation, fold 2 out of 2
#> Computing chain 1
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#> Cross-validation, fold 1 out of 2
#> Computing chain 1
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#> Chain 2, iteration 10000 of 10500 (sampling)
#> Cross-validation, fold 1 out of 2
#> Computing chain 1
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#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
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#> Cross-validation, fold 2 out of 2
#> Computing chain 1
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#> Computing chain 2
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#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
```

```
result
#>             [,1]      [,2]      [,3]      [,4]
#> [1,]  0.88284778 0.9996170 0.9851035 0.9848477
#> [2,] -0.04489961 0.6424797 0.5247010 0.5263619
#> [3,]  0.01996118 0.8703277 0.4845272 0.4777726
```

We can see that the $|E_t - x_{i,t}|$ and $|x_{t+1} - x_{i,t}|$ do have similar explanatory power, however, the species traits were in fact the stronger predictor of species abundances. I finally ask whether a model with raw trait values and change in trait values has imprived explanatory power (if the magnitude of evolutionary change has any additional explanatory role).

```
# Design and fit 4 alternative HMSC models
XFormula = ~E+Esq+x1+x2+dx1+dx2
models[[5]] = Hmsc(Y = Y, XData = XData, XFormula = XFormula, studyDesign = studyDesign, ranLevels = li
models[[5]] =sampleMcmc(models[[5]],thin=thin,sample=samples,transient=transient,nChains=nChains,verbos
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
#> Chain 1, iteration 5000 of 10500 (sampling)
#> Chain 1, iteration 7500 of 10500 (sampling)
#> Chain 1, iteration 10000 of 10500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
#> Chain 2, iteration 5000 of 10500 (sampling)
#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
#> Failed updaters and their counts in chain 1  ( 10500  attempts):
#> GammaEta
#>    10012
#> Failed updaters and their counts in chain 2  ( 10500  attempts):
#> GammaEta
#>    10041
```

```
# Explanatory power
result2 <- matrix(NA,nrow=3,ncol=5)
result2[,1:4] <- result
for(i in 5){
  m = models[[i]]
  # Explanatory power
  preds = computePredictedValues(m)
  MF = evaluateModelFit(hM=m,predY=preds)
  result2[1,i] = mean(MF$R2)
  # Predictive power based on cross-validation
  preds = computePredictedValues(m,partition=partition)
  MF = evaluateModelFit(hM=m,predY=preds)
  result2[2,i] <- mean(MF$R2)
  # Predictive power based on conditional cross-validation
  preds = computePredictedValues(m,partition=partition,partition.sp=partition.sp,mcmcStep=100)
  MF = evaluateModelFit(hM=m,predY=preds)
  result2[3,i] = mean(MF$R2)
}
#> Cross-validation, fold 1 out of 2
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
#> Chain 1, iteration 5000 of 10500 (sampling)
#> Chain 1, iteration 7500 of 10500 (sampling)
#> Chain 1, iteration 10000 of 10500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
#> Chain 2, iteration 5000 of 10500 (sampling)
#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
#> Failed updaters and their counts in chain 1  ( 10500  attempts):
#> GammaEta
#>    10467
#> Failed updaters and their counts in chain 2  ( 10500  attempts):
#> GammaEta
#>    10466
#> Cross-validation, fold 2 out of 2
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
#> Chain 1, iteration 5000 of 10500 (sampling)
#> Chain 1, iteration 7500 of 10500 (sampling)
#> Chain 1, iteration 10000 of 10500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
#> Chain 2, iteration 5000 of 10500 (sampling)
#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
#> Failed updaters and their counts in chain 1  ( 10500  attempts):
#> GammaEta
#>    10500
#> Failed updaters and their counts in chain 2  ( 10500  attempts):
#> GammaEta
#>    10500
#> Cross-validation, fold 1 out of 2
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
#> Chain 1, iteration 5000 of 10500 (sampling)
#> Chain 1, iteration 7500 of 10500 (sampling)
#> Chain 1, iteration 10000 of 10500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
#> Chain 2, iteration 5000 of 10500 (sampling)
#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
#> Failed updaters and their counts in chain 1  ( 10500  attempts):
#> GammaEta
#>    10470
#> Failed updaters and their counts in chain 2  ( 10500  attempts):
#> GammaEta
#>    10468
#> Cross-validation, fold 2 out of 2
#> Computing chain 1
#> Chain 1, iteration 2500 of 10500 (sampling)
#> Chain 1, iteration 5000 of 10500 (sampling)
#> Chain 1, iteration 7500 of 10500 (sampling)
#> Chain 1, iteration 10000 of 10500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 10500 (sampling)
#> Chain 2, iteration 5000 of 10500 (sampling)
#> Chain 2, iteration 7500 of 10500 (sampling)
#> Chain 2, iteration 10000 of 10500 (sampling)
#> Failed updaters and their counts in chain 1  ( 10500  attempts):
#> GammaEta
#>    10500
#> Failed updaters and their counts in chain 2  ( 10500  attempts):
#> GammaEta
#>    10500
```

```
knitr::knit_exit()
```