Appendix S1. Linear regression models and non-linear population dynamics

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1 One species, logistic growth

Population growth over time in a single species is first modelled using a Beverton-Holt (discrete-time, logistic) model (Beverton and Holt (1957)), using an intra-specific competition coefficient for density-dependent growth (Hart and Marshall (2013)) - thus $\alpha = 1/K$.

$$N_{i,t+1} = \frac{r_i N_{i,t}}{1 + \alpha_{ii} N_{i,t}}$$

Note that in this model, the system is at equilibrium when $N_{i,t+1} = N_{i,t}$, and therefore:

$$N^* = N^* \frac{r_i}{1 + \alpha_{ii} N^*}$$

$$1 = \frac{r_i}{1 + \alpha_{ii} N^*}$$

$$N^* = \frac{r_i - 1}{\alpha_{ii}}$$

1.1 Population dynamics simulation

In the metacommunity simulation in the main text, a species resides in a site with an initial population size $N_{i,0} \sim Pois(10)$, a growth rate r_i that depends on the local environmental value E_k and the species trait x_i, and a fixed intra-specific competition coefficient of $\alpha_{ii} = 0.00125$. We simulate population growth here:

```
set.seed(42)
# Simulate initial species population growth
N1.0 <- rpois(1, 10)
r1.0 <- 1.67
alpha.11 <- 0.00125
# model function
disc_log <- function(r, N0, alpha) {
    Nt1 <- (r * N0)/(1 + alpha * N0)
```

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```
    return(Nt1)
}
# Simulation of model for t time steps
t <- 30
N <- rep(NA, t)
N[1] <- N1.0
for (i in 2:t) {
    N[i] <- disc_log(r = r1.0, N0 = N[i - 1], alpha = alpha.11)
}
```

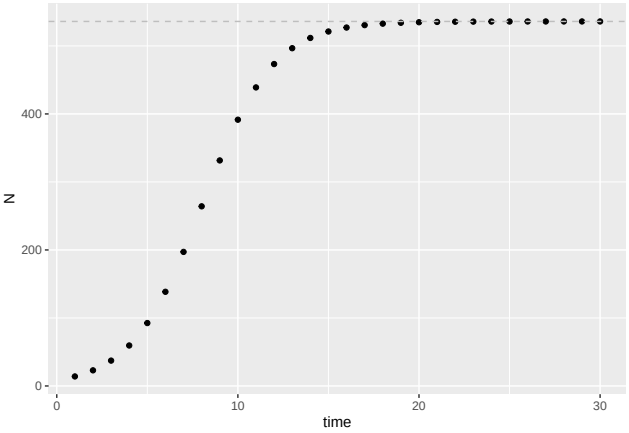


Figure 1: Population size N over time t for a discrete-time logistic growth model, with parameters $r_i = 1.67$, $N_{1,0} = 14$, and $\alpha_{11} = 0.00125$.

1.2 Linear statistical model

We fit the population time series data to a first-order auto-regressive model to predict N_{t+1} as a function of N_t, and compare that to a linear regression. We use ln-N after Ives (1995), as also discussed in Certain et al. (2018) and Olivença et al. (2021).

$$N_{t+1} = \beta_0 + \beta_1 N_t + \epsilon_t$$

```
# Fit the model
m.1.ar <- arima(x = log(N), order = c(1, 0, 0), include.mean = T, method = "CSS")
m.1.lm <- lm(log(dat$N[2:t]) ~ log(dat$N[1:(t - 1)]))
# plotting the series along with the fitted values
m.1.ar.fit <- log(N) - residuals(m.1.ar)
m.1.lm.fit <- log(dat$N[2:t]) - m.1.lm$resid
dat$ar1.fit <- m.1.ar.fit
dat$lm.fit <- NA
dat$lm.fit[2:t] <- m.1.lm.fit
```

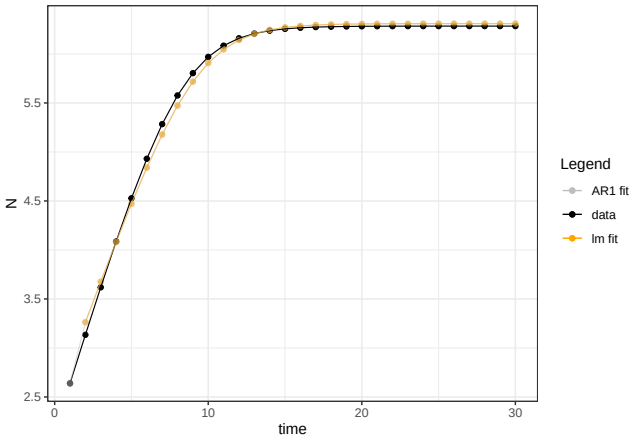


Figure 2: Population size over time (black line) with fitted values from a first-order autoregressive model (red dashed line).

18 The linear model is a good fit, and N_{t+1} and N_t are well-represented by a linear function:

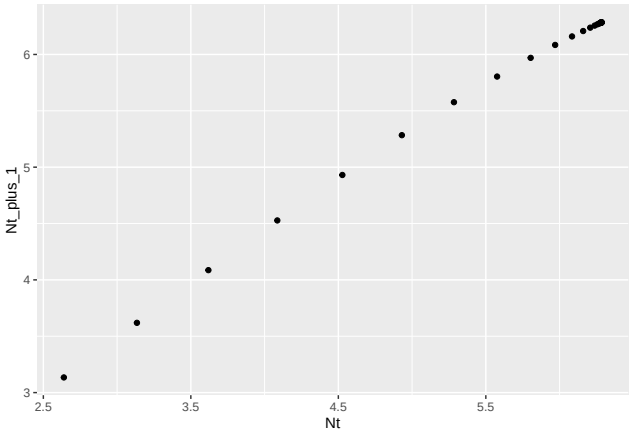


Figure 3: Population size (logarithm) at one time step N_{t+1} as a function of log-population size in the previous time step N_t.

19 We also examine density dependence by plotting $\Delta N = N_{t+1} - N_t$ vs. N_t:

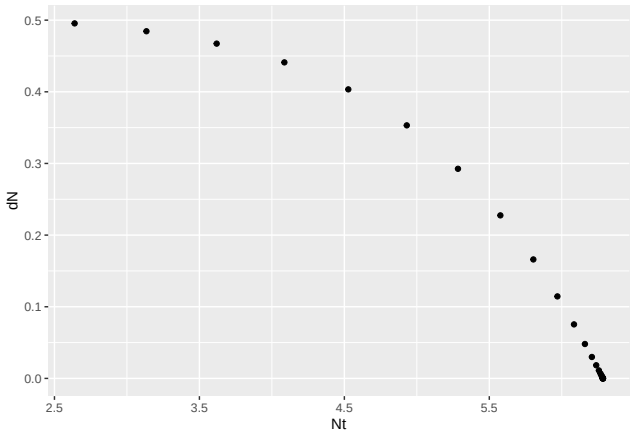


Figure 4: Change in population size from one time step to the next N_{t+1} as a function of N_{t+1}

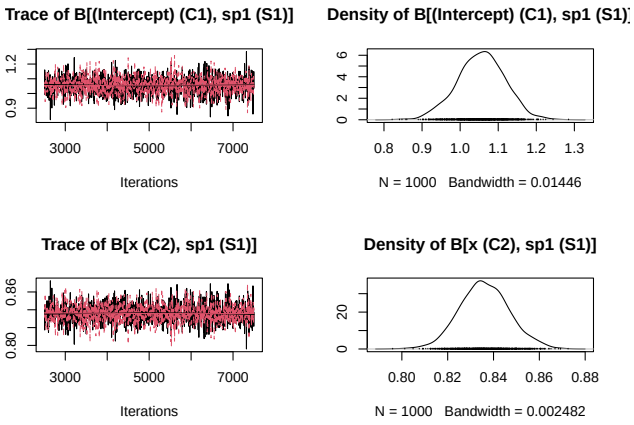
1.3 Bayesian linear statistical model: HMSC

We can estimate the same model parameters using HMSC:

```
# prepare data in HMSC format
Y <- as.matrix(log(dat$N[2:t]))
XData <- data.frame(x = log(dat$N[1:(t - 1)]))
m.1.hmsc <- Hmsc(Y = Y, XData = XData, XFormula = ~x)
# Bayesian model parameters
nChains <- 2
thin <- 5
samples <- 1000
transient <- 500 * thin
verbose <- 500 * thin
# sample MCMC
m.1.sample <- sampleMcmc(m.1.hmsc, thin = thin, sample = samples, transient = transient,
    nChains = nChains, verbose = verbose)
#> setting updater$GammaEta=FALSE due to absence of random effects included to the model
#> Computing chain 1
#> Chain 1, iteration 2500 of 7500 (transient)
#> Chain 1, iteration 5000 of 7500 (sampling)
#> Chain 1, iteration 7500 of 7500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 7500 (transient)
#> Chain 2, iteration 5000 of 7500 (sampling)
#> Chain 2, iteration 7500 of 7500 (sampling)
```

```
m.post.hmsc <- convertToCodaObject(m.1.sample)
summary(m.post.hmsc$Beta)
#>
#> Iterations = 2505:7500
#> Thinning interval = 5
#> Number of chains = 2
#> Sample size per chain = 1000
#>
#> 1. Empirical mean and standard deviation for each variable,
```

```
#>    plus standard error of the mean:
#>
#>                                    Mean      SD  Naive SE Time-series SE
#> B[(Intercept) (C1), sp1 (S1)] 1.0550 0.06240 0.0013952      0.0013954
#> B[x (C2), sp1 (S1)]           0.8361 0.01083 0.0002422      0.0002415
#>
#> 2. Quantiles for each variable:
#>
#>                                    2.5%    25%    50%    75%  97.5%
#> B[(Intercept) (C1), sp1 (S1)] 0.9288 1.0132 1.0564 1.0974 1.1693
#> B[x (C2), sp1 (S1)]           0.8154 0.8287 0.8358 0.8431 0.8582
plot(m.post.hmsc$Beta)
```



These estimates match well with those from the AR1 and linear model:

```
# AR1 coefficients (recall that the intercept is the term below multipled by 1
# - phi1)
m.1.ar$coef
#>       ar1 intercept
#> 0.8359839 6.4371388
m.1.ar$coef[2] * (1 - m.1.ar$coef[1])
#> intercept
#>  1.055794
# linear model
summary(m.1.lm)$coefficients[1:2, 1:2]
#>                       Estimate  Std. Error
#> (Intercept)          1.0557944 0.054425861
#> log(dat$N[1:(t - 1)]) 0.8359839 0.009441702
# Bayesian estimates
summary(m.post.hmsc$Beta)$statistics[1:2, 1:2]
#>                                    Mean         SD
#> B[(Intercept) (C1), sp1 (S1)] 1.0549596 0.06239605
#> B[x (C2), sp1 (S1)]           0.8360545 0.01082936
```

```
Gradient <- constructGradient(m.1.sample, focalVariable = "x", ngrid = 29)
predY <- predict(m.1.sample, Gradient = Gradient, expected = TRUE)
# preds <-computePredictedValues(m.1.sample)
plotGradient(m.1.sample, Gradient, pred = predY, showData = T, measure = "Y", main = "",
    xlab = "N_t", ylab = "predicted N_t+1")
```

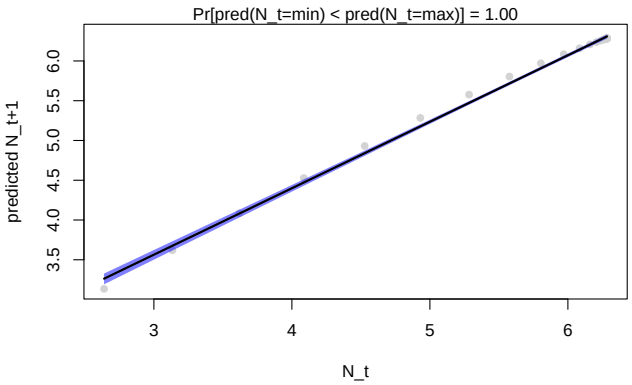
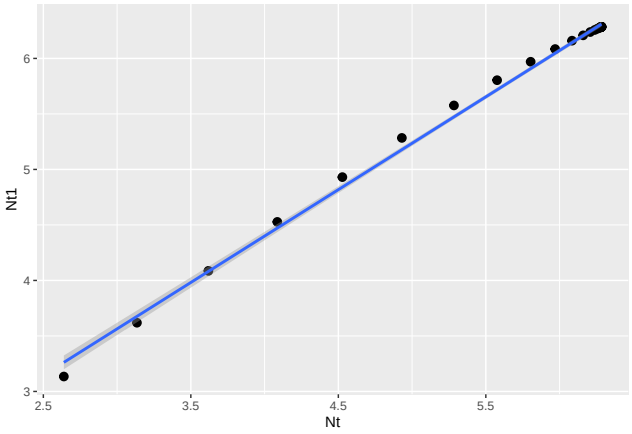


Figure 5: Observed (grey) and model-fit (blue) values for population size at time t (x-axis) and t+1 (y-axis).

```
lm_dat <- data.frame(cbind(log(dat$N[2:t]), log(dat$N[1:(t - 1)])))
colnames(lm_dat) <- c("Nt1", "Nt")
ggplot(lm_dat, aes(Nt, Nt1)) + stat_summary(fun.data = mean_cl_normal) + geom_smooth(method = "lm")
#> `geom_smooth()` using formula = 'y ~ x'
#> Warning: Removed 29 rows containing missing values (`geom_segment()`).
```



1.4 Conclusions

In this example, a first-order auto-regressive model works well, bypassing the need to estimate logistic growth parameters r_i and α_{ii}. The density-dependence dynamics ($\Delta N \sim f(N_t)$) show an overall declining trend over time. The Bayesian estimation implemented in HMSC gives good parameter estimates.

2 One species, logistic growth, environmental covariate

We now consider using a linear model to analyze population growth when the species growth rate is impacted by a single environmental covariate.

2.1 Growth depends on environment

First we add environment-dependent growth rate. The growth rate r_i becomes:

$$r_i = \hat{W} e^{-(E - x_{i,t})^2}$$

Here, $\hat{W}$ is the maximal population growth rate (set to 1.67 as above), E is the local environmental trait optimum value, and $x_{i,t}$ is species i trait value at time t. We see that if $E = x_{i,t}$ then the growth rate is at the value $r = 1.67$. Here, we begin with $E = x_{i,t} = 0.8$, then simulate the environment E value fluctuating randomly over time, and finally use a linear model to fit E as a covariate.

```
# Simulate initial species population growth with environment fluctuations
N1.0 <- 10
r1.0 <- 1.67
alpha.11 <- 0.00125
E.0 <- 0.8
x1.0 <- 0.8
# model function
disc_log_E <- function(r, N0, alpha, E, x) {
    Nt1 <- ((r * exp(-(E - x)^2)) * N0)/(1 + alpha * N0)
    return(Nt1)
}
# Simulation of model for t time steps
t <- 40
N <- rep(NA, t)
N[1] <- N1.0
E <- rep(NA, t)
E[1] <- E.0
for (i in 2:t) {
    N[i] <- disc_log_E(r = r1.0, N0 = N[i - 1], alpha = alpha.11, E = E[i - 1], x = x1.0)
    E[i] <- E[i - 1] + rnorm(1, 0, 0.1)
}
```

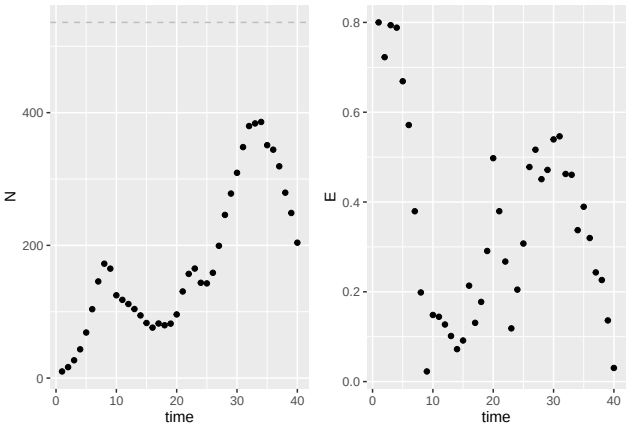


Figure 6: Population size N over time t for a discrete-time logistic growth model, with parameters $r_i = 1.67$, $N_{1,0} = 14$, and $\alpha_{11} = 0.00125$. Relationship between E and Nt is also shown.

2.2 Linear statistical model with environmental covariate

We now include environment E as a covariate in the linear model:

$$N_t = \beta_0 + \beta_1 N_{t-1} + \beta_2 E_{t-1} + \epsilon_t$$

```
# Fit the model
m.2.ar <- arima(x = log(N), order = c(1, 0, 0), include.mean = T, method = "CSS",
    xreg = E)
m.2.lm <- lm(log(dat$N[2:t]) ~ log(dat$N[1:(t - 1)]) + log(E[1:(t - 1)]))
# plotting the series along with the fitted values
m.2.ar.fit <- log(N) - residuals(m.2.ar)
m.2.lm.fit <- log(dat$N[2:t]) - m.2.lm$resid
dat$ar2.fit <- m.2.ar.fit
dat$lm2.fit <- NA
dat$lm2.fit[2:t] <- m.2.lm.fit
```

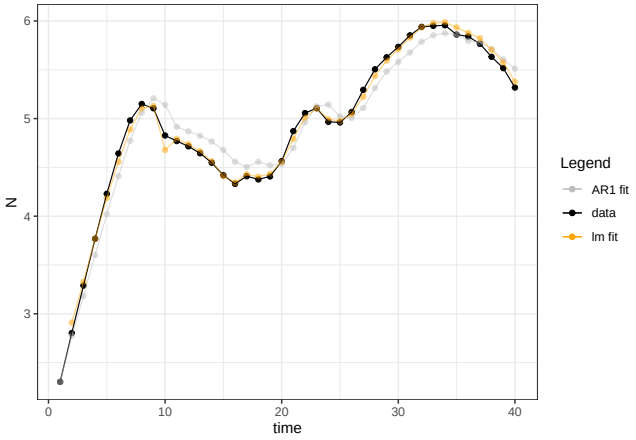


Figure 7: Population size over time (black line) with fitted values from a first-order autoregressive model (red dashed line).

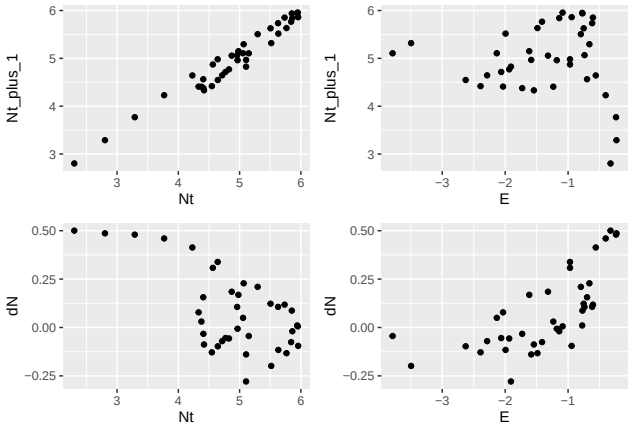


Figure 8: Population size (logarithm) at one time step N_{t+1} as a function of log-population size in the previous time step N_t.

The linear model is a good fit when including the environmental covariate. N_{t+1} and N_t can still be captured by a linear relationship. However we see that the relationship between N_{t+1} and E_t is non-linear. This tells us that the lm is good for predictions, but not for inference (for capturing well the relationsip between the predictor and response variable). The use of linear relationships in JSDMs is discussed in (Ingram et al. 2020), and in many applications (e.g. (Erickson and Smith 2023)) quadratic terms are used, which create bell-shaped response curves that may better match species with optimal niches (as opposed to linear,

46 monotonically increasing relationships between population size and environmental predictors). We thus
47 include a quadratic term for E_t to provide a better fit to the data.

```
df <- data.frame(cbind(log(dat$N[2:t]), log(dat$N[1:(t - 1)]), E[1:(t - 1)], E[1:(t -
    1)]^2))
colnames(df) <- c("Nt1", "Nt", "E", "Esq")
m.2.lm <- lm(Nt1 ~ Nt + E + Esq, data = df)
```

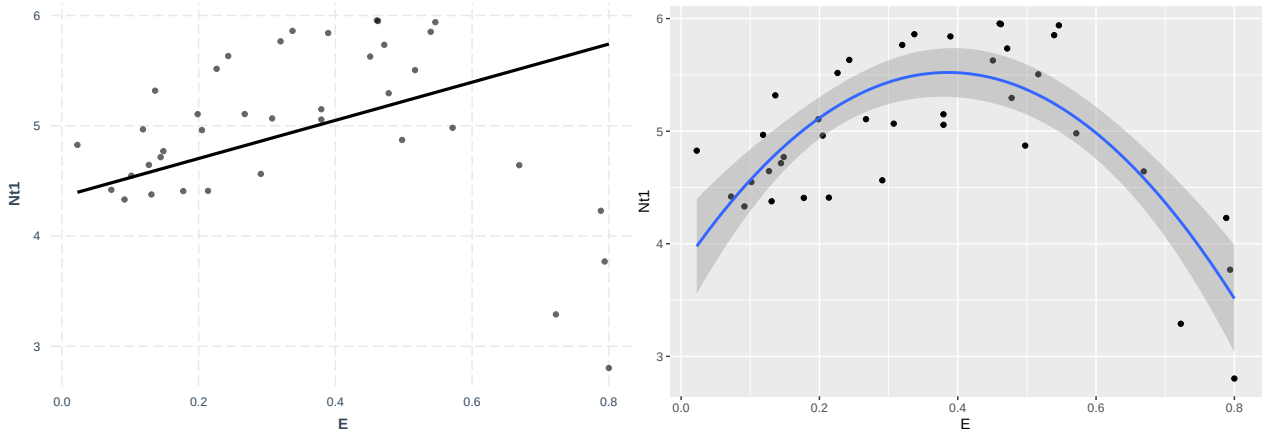


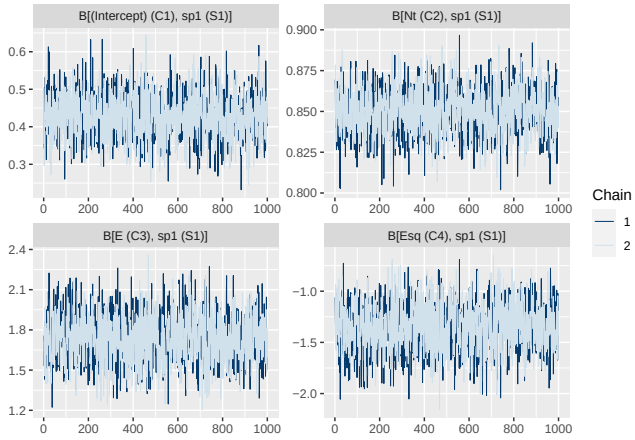
Figure 9: Population size (logarithm) at one time step N_{t+1} as a function of log-population size in the previous time step N_t.

48 ## 2.3 Bayesian linear statistical model: HMSC

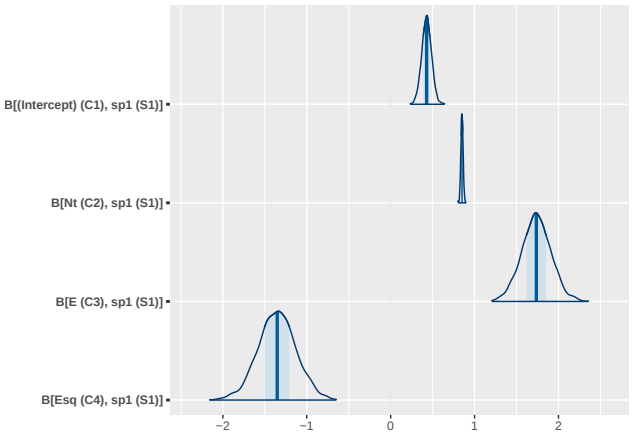
49 We can estimate the same model parameters using HMSC:

```
# prepare data in HMSC format
Y <- as.matrix(log(dat$N[2:t]))
XData <- df
m.2.hmsc <- Hmsc(Y = Y, XData = XData, XFormula = ~Nt + E + Esq)
# Bayesian model parameters
nChains <- 2
thin <- 5
samples <- 1000
transient <- 500 * thin
verbose <- 500 * thin
# sample MCMC
m.2.sample <- sampleMcmc(m.2.hmsc, thin = thin, sample = samples, transient = transient,
    nChains = nChains, verbose = verbose)
#> setting updater$GammaEta=FALSE due to absence of random effects included to the model
#> Computing chain 1
#> Chain 1, iteration 2500 of 7500 (transient)
#> Chain 1, iteration 5000 of 7500 (sampling)
#> Chain 1, iteration 7500 of 7500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 7500 (transient)
#> Chain 2, iteration 5000 of 7500 (sampling)
#> Chain 2, iteration 7500 of 7500 (sampling)
```

```
m2.post.hmsc <- convertToCodaObject(m.2.sample)
summary(m2.post.hmsc$Beta)
#>
#> Iterations = 2505:7500
#> Thinning interval = 5
#> Number of chains = 2
#> Sample size per chain = 1000
#>
#> 1. Empirical mean and standard deviation for each variable,
#>    plus standard error of the mean:
#>
#>                                    Mean      SD  Naive SE Time-series SE
#> B[(Intercept) (C1), sp1 (S1)]  0.4287 0.05840 0.0013059      0.0013051
#> B[Nt (C2), sp1 (S1)]           0.8500 0.01357 0.0003034      0.0003136
#> B[E (C3), sp1 (S1)]            1.7365 0.17407 0.0038922      0.0039946
#> B[Esq (C4), sp1 (S1)]         -1.3544 0.22541 0.0050403      0.0051805
#>
#> 2. Quantiles for each variable:
#>
#>                                   2.5%     25%     50%    75%   97.5%
#> B[(Intercept) (C1), sp1 (S1)]  0.3125  0.3902  0.4285  0.467  0.5435
#> B[Nt (C2), sp1 (S1)]           0.8235  0.8413  0.8500  0.859  0.8768
#> B[E (C3), sp1 (S1)]            1.3967  1.6194  1.7361  1.853  2.0816
#> B[Esq (C4), sp1 (S1)]         -1.8157 -1.5001 -1.3518 -1.207 -0.9151
bayesplot::mcmc_trace(m2.post.hmsc$Beta)
```




```
bayesplot::mcmc_areas(m2.post.hmsc$Beta, area_method = c("equal height"))
```



These estimates match well with those from the AR1 and linear model:

```
# AR1 coefficients (recall that the intercept is the term below multipled by 1
# - phi1)
m.2.ar$coef
#>        ar1  intercept          E
#>  0.8471120  5.4224546 -0.1096173
m.2.ar$coef[2] * (1 - m.2.ar$coef[1])
#> intercept
#>  0.829028
# linear model
summary(m.2.lm)$coefficients[1:4, 1:2]
#>               Estimate Std. Error
#> (Intercept)  0.4286437 0.04917405
#> Nt           0.8502417 0.01151860
#> E            1.7296394 0.14595151
#> Esq         -1.3462240 0.18902070
# Bayesian estimates
summary(m2.post.hmsc$Beta)$statistics[1:4, 1:2]
#>                                      Mean         SD
#> B[(Intercept) (C1), sp1 (S1)]  0.4287409 0.05840051
#> B[Nt (C2), sp1 (S1)]           0.8500472 0.01356690
#> B[E (C3), sp1 (S1)]            1.7365191 0.17406609
#> B[Esq (C4), sp1 (S1)]         -1.3543664 0.22541119
```

We recall that the interpretation of the coefficients in an arimaX (arima with covariates) model is difficult. They do not give the impact on N_t per unit increase in X as in a regression. So we do not interpret the causation implied by the coefficient in the arimaX model. In the regression model, we can see that E has a positive impact on N_t.

```
Gradient <- constructGradient(m.2.sample, focalVariable = "E", non.focalVariables = list(Nt = list(2),
    Esq = list(2)), ngrid = 39)
predY <- predict(m.2.sample, XData = Gradient$XDataNew, expected = TRUE)
plotGradient(m.2.sample, Gradient, pred = predY, showData = T, measure = "Y", main = "",
    xlab = "E_t", ylab = "predicted N_t+1")
# Can't figure out curved gradient using E and E^2 pr <-
# predict(m.2.hmsc,m.2.sample,)
```

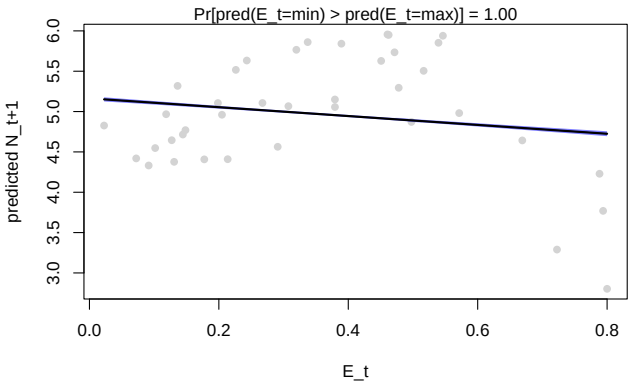


Figure 10: Observed (grey) and model-fit (blue) values for population size at time t (x-axis) and t+1 (y-axis).

2.4 Conclusions

In this example, the linear regression again works well to describe the impact of E_t for N_t when using the quadratic formulation. The arimaX model works well for fitting and subsequent prediction, but less well for inference about the impacts of E. From the quadratic regression terms for E, we correctly see that the population size is maximal at the species trait value and decreases away from that value. We will continue to use log-transformed abundance and now introduce quadratic terms for the environmental parameter.

3 Two species, logistic growth, competition

XXXXX ## Interspecific competition The growth equation for each species now becomes:

$$N_{i,t+1} = \frac{r_i N_{i,t}}{1 + \alpha_{ii} N_{i,t} + \alpha_{ij} N_{j,t}}$$

We use a distinct growth rate for the 2nd species and introduce the interspecific interaction coefficient α_{ij}.

```
# Simulate initial species population growth with environment fluctuations
N1.0 <- 10
N2.0 <- 10
r1.0 <- 1.67
r2.0 <- 1.7
alpha.11 <- 0.00125
alpha.22 <- 0.00125
alpha.12 <- 0.008
alpha.21 <- 0.008725
# model function
disc_LV_comp <- function(r1, r2, N1.0, N2.0, alpha.11, alpha.22, alpha.12, alpha.21) {
    Nt1 <- (r1 * N1.0)/(1 + alpha.11 * N1.0 + alpha.12 * N2.0)
    Nt2 <- (r2 * N2.0)/(1 + alpha.22 * N2.0 + alpha.21 * N1.0)
    return(c(Nt1, Nt2))
}
# 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")
N$N1[1] <- N1.0
N$N2[1] <- N2.0
for (i in 2:t) {
    res <- disc_LV_comp(r1 = r1.0, r2 = r2.0, N1.0 = N[i - 1, 1], N2.0 = N[i - 1,
        2], alpha.11 = alpha.11, alpha.22 = alpha.22, alpha.12 = alpha.12, alpha.21 = alpha.21)
    N$N1[i] <- res[1]
    N$N2[i] <- res[2]
}
```

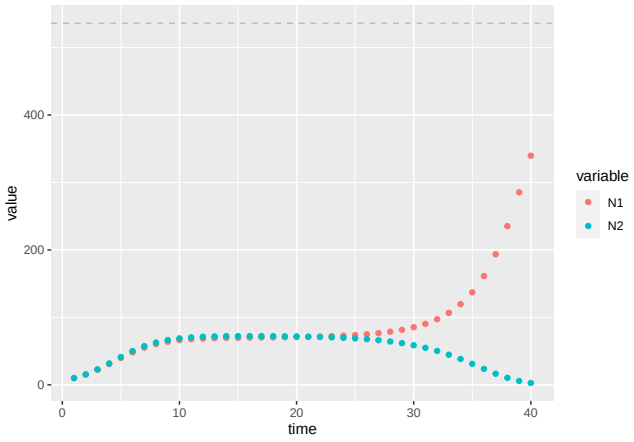


Figure 11: Population size N over time t for a discrete-time logistic growth model, with parameters $r_i = 1.67$, $N_{1,0} = 14$, and $\alpha_{11} = 0.00125$. Relationship between E and Nt is also shown.

3.1 Linear statistical model with environmental covariate

We fit each species' population time series to an arimaX and lm with population size of the others species as a covariate.

$$N_{1,t} = \beta_0 + \beta_1 N_{1,t-1} + \beta_2 N_{2,t-1} + \epsilon_t$$

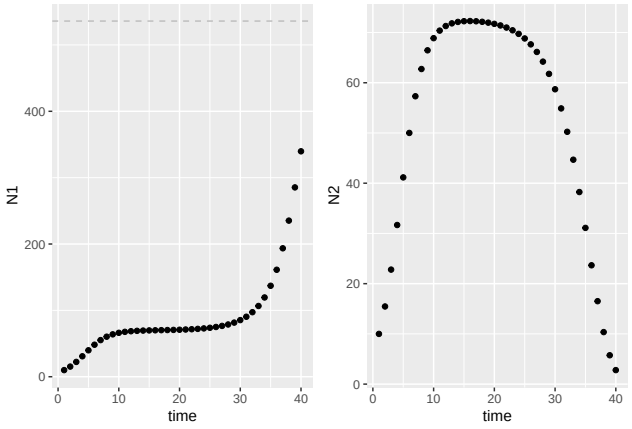


Figure 12: Population size N over time t for a discrete-time logistic growth model, with parameters $r_i = 1.67$, $N_{1,0} = 14$, and $\alpha_{11} = 0.00125$. Relationship between E and Nt is also shown.

```
## Fit the model for Species 1
m.3.ar.n1 <- arima(x = log(N$N1), order = c(1, 0, 0), include.mean = T, method = "CSS",
    xreg = N$N2)
m.3.lm.n1 <- lm(log(dat$N1[2:t]) ~ log(dat$N1[1:(t - 1)]) + log(dat$N2[1:(t - 1)]))
# plotting the series along with the fitted values
m.3.ar.fit.n1 <- log(N$N1) - residuals(m.3.ar.n1)
m.3.lm.fit.n1 <- log(dat$N1[2:t]) - m.3.lm.n1$resid
dat$ar3.fit.n1 <- m.3.ar.fit.n1
dat$lm3.fit.n1 <- NA
dat$lm3.fit.n1[2:t] <- m.3.lm.fit.n1
## Species 2
m.3.ar.n2 <- arima(x = log(N$N2), order = c(1, 0, 0), include.mean = T, method = "CSS",
    xreg = N$N1)
m.3.lm.n2 <- lm(log(dat$N2[2:t]) ~ log(dat$N2[1:(t - 1)]) + log(dat$N1[1:(t - 1)]))
# plotting the series along with the fitted values
m.3.ar.fit.n2 <- log(N$N2) - residuals(m.3.ar.n2)
m.3.lm.fit.n2 <- log(dat$N2[2:t]) - m.3.lm.n2$resid
dat$ar3.fit.n2 <- m.3.ar.fit.n2
dat$lm3.fit.n2 <- NA
dat$lm3.fit.n2[2:t] <- m.3.lm.fit.n2
```

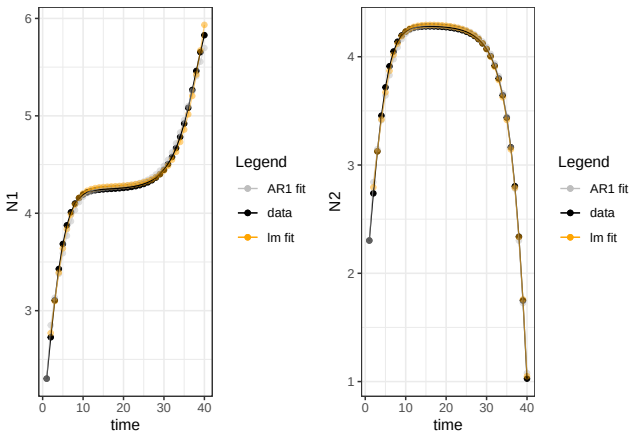


Figure 13: Population size over time (black line) with fitted values from a first-order autoregressive model (red dashed line).

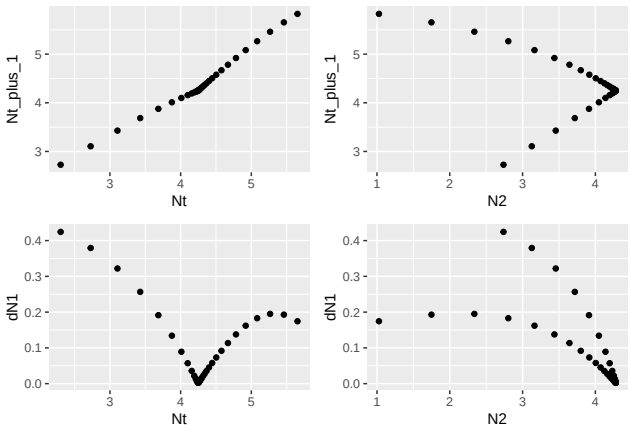
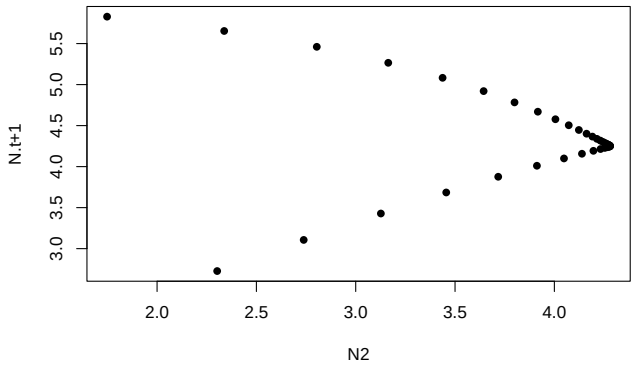


Figure 14: Population size (logarithm) at one time step N_{t+1} as a function of log-population size in the previous time step N_t.

69 XXXXX

```
df <- data.frame(cbind(log(dat$N1[2:t]), log(dat$N1[1:(t - 1)]), log(dat$N2[1:(t -
    1)])))
colnames(df) <- c("Nt1", "N1", "N2")
m.3.lm <- lm(Nt1 ~ I(1/N1) + I(1/N2), data = df)

cor(df$Nt1, predict(m.3.lm))
#> [1] 0.9845708
summary(m.3.lm)
#>
#> Call:
#> lm(formula = Nt1 ~ I(1/N1) + I(1/N2), data = df)
#>
#> Residuals:
#>      Min       1Q   Median       3Q      Max
#> -0.30952 -0.04467 -0.03442  0.03430  0.22447
#>
#> Coefficients:
#>             Estimate Std. Error t value Pr(>|t|)
#> (Intercept)   6.4056     0.1060   60.45  < 2e-16 ***
#> I(1/N1)     -12.2863     0.3774  -32.55  < 2e-16 ***
#> I(1/N2)       3.3309     0.2448   13.61 9.24e-16 ***
#> ---
#> Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
#>
#> Residual standard error: 0.1063 on 36 degrees of freedom
#> Multiple R-squared:  0.9694, Adjusted R-squared:  0.9677
#> F-statistic: 569.8 on 2 and 36 DF,  p-value: < 2.2e-16
xx <- seq(0, 100, length = 1000)
prediction <- data.frame(N2 = xx, N1 = 100)
plot(df$N2, df$Nt1, xlab = "N2", ylab = "N.t+1", pch = 16)
lines(prediction$N2, predict(m.3.lm, prediction), lty = 2, col = "red", lwd = 3)
```




```
#> Using data df from global environment. This could cause incorrect results
#> if df has been altered since the model was fit. You can manually provide
#> the data to the "data =" argument.
```

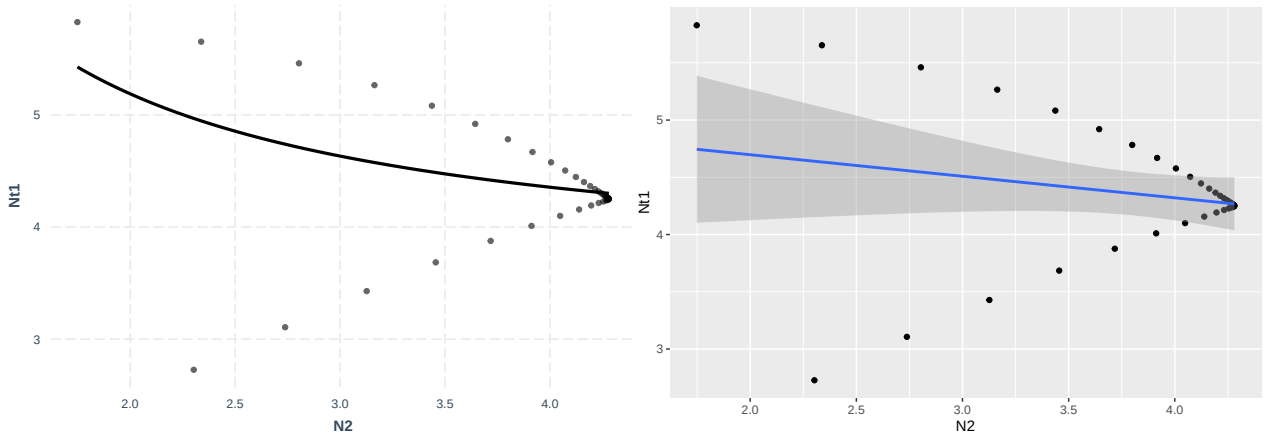


Figure 15: Population size (logarithm) at one time step N_{t+1} as a function of log-population size in the previous time step N_t.

We can already see that the linear model does not provide a useful fit to the data points (neither does taking the inverse function help). The regression parameters can predict well the population size of the other species, but they are not informative for inference. This has been observed previously (Certain et al. (2018)), and non-linear least squares models (among others) are more often used to estimate parameters for dynamics resulting from these kinds of species interaction models (Kloppers and Greeff (2013); Mühlbauer et al. (2020); Olivença et al. (2021)). The inability of the linear models to reproduce the interaction coefficients is more clearly demonstrated in Certain et al. (2018). However, they do indicate that the slope of the linear model can reflect the direction of effect for the interacting species.

Instead of further exploring techniques to fit to time-series derived from non-linear competition processes, we look more closely at how HMSC manages to fit data emerging from competition dynamics and make inference about species interactions. Instead of estimating full interaction coefficients, or assuming sparse interactions, they instead assume that a reduced number of linear combinations of species abundances that are most relevant to determining future growth rates for species in the community can bypass the 'curse of dimensionality' problem. This is well presented in Ovaskainen et al. (2017). We apply that approach here:

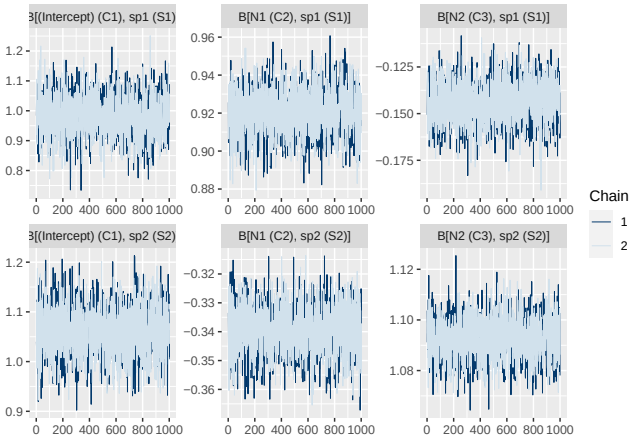
3.2 Bayesian linear statistical model: HMSC

We can fit the data to a linear model using HMSC, with latent variables to capture the species associations. These are implemented by including a random effect at the time level.

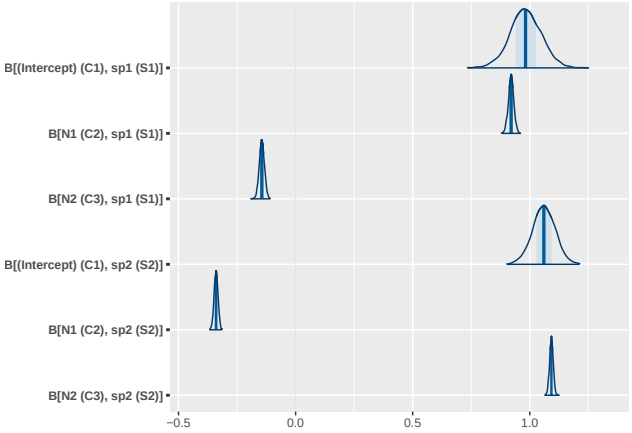
```
# prepare data in HMSC format
Y <- as.matrix(cbind(log(dat$N1[2:t]), log(dat$N2[2:t])))
XData <- df[, 2:3]
studyDesign = data.frame(sample = as.factor(1:(t - 1)))
rL = HmscRandomLevel(units = studyDesign$sample)
m.3.hmsc = Hmsc(Y = Y, XData = XData, studyDesign = studyDesign, ranLevels = list(sample = rL))
# Bayesian model parameters
nChains <- 2
thin <- 5
samples <- 1000
transient <- 500 * thin
verbose <- 500 * thin
# sample MCMC
m.3.sample <- sampleMcmc(m.3.hmsc, thin = thin, sample = samples, transient = transient,
    nChains = nChains, verbose = verbose)
#> Computing chain 1
#> Chain 1, iteration 2500 of 7500 (transient)
#> Chain 1, iteration 5000 of 7500 (sampling)
#> Chain 1, iteration 7500 of 7500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 7500 (transient)
#> Chain 2, iteration 5000 of 7500 (sampling)
#> Chain 2, iteration 7500 of 7500 (sampling)
```

```
m3.post.hmsc <- convertToCodaObject(m.3.sample)
summary(m3.post.hmsc$Beta)
#>
#> Iterations = 2505:7500
#> Thinning interval = 5
#> Number of chains = 2
#> Sample size per chain = 1000
#>
#> 1. Empirical mean and standard deviation for each variable,
#>    plus standard error of the mean:
#>
#>                                    Mean       SD  Naive SE Time-series SE
#> B[(Intercept) (C1), sp1 (S1)]  0.9829 0.067231 0.0015033      0.0015031
#> B[N1 (C2), sp1 (S1)]           0.9202 0.011671 0.0002610      0.0002610
#> B[N2 (C3), sp1 (S1)]          -0.1442 0.011042 0.0002469      0.0002516
#> B[(Intercept) (C1), sp2 (S2)]  1.0606 0.048507 0.0010846      0.0010845
#> B[N1 (C2), sp2 (S2)]          -0.3398 0.008349 0.0001867      0.0001867
#> B[N2 (C3), sp2 (S2)]           1.0926 0.007894 0.0001765      0.0001827
#>
#> 2. Quantiles for each variable:
#>
#>                                   2.5%     25%     50%     75%   97.5%
#> B[(Intercept) (C1), sp1 (S1)]  0.8470  0.9394  0.9820  1.0269  1.1174
#> B[N1 (C2), sp1 (S1)]           0.8973  0.9129  0.9205  0.9278  0.9432
#> B[N2 (C3), sp1 (S1)]          -0.1653 -0.1514 -0.1442 -0.1369 -0.1226
```

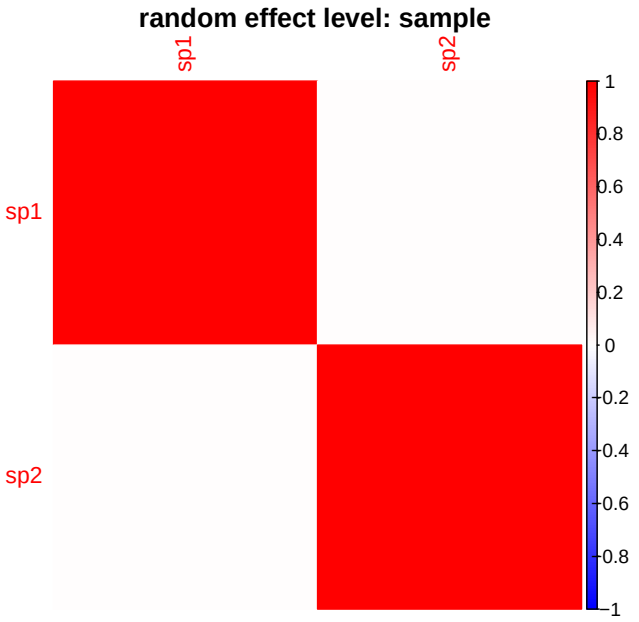
```
#> B[(Intercept) (C1), sp2 (S2)]  0.9638  1.0285  1.0603  1.0938  1.1557
#> B[N1 (C2), sp2 (S2)]          -0.3563 -0.3455 -0.3397 -0.3339 -0.3235
#> B[N2 (C3), sp2 (S2)]           1.0772  1.0874  1.0926  1.0977  1.1080
bayesplot::mcmc_trace(m3.post.hmsc$Beta)
```




```
bayesplot::mcmc_areas(m3.post.hmsc$Beta, area_method = c("equal height"))
```




```
OmegaCor = computeAssociations(m.3.sample)
supportLevel = 0.95
toPlot = ((OmegaCor[[1]]$support > supportLevel) + (OmegaCor[[1]]$support < (1 -
    supportLevel)) > 0) * OmegaCor[[1]]$mean
corrplot::corrplot(toPlot, method = "color", col = colorRampPalette(c("blue", "white",
    "red"))(200), title = paste("random effect level:", m.3.sample$rLNames[1]), mar = c(0,
    0, 1, 0))
```



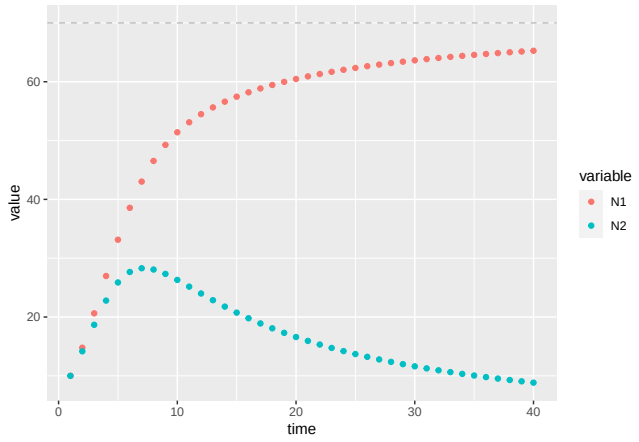
These estimates match well with those from the AR1 and linear model:

```
# AR1 coefficients (recall that the intercept is the term below multipled by 1
# - phi1)
m.3.ar.n1$coef
#>         ar1   intercept        N$N2
#>  0.79696422  5.69840619 -0.01881979
m.3.ar.n1$coef[2] * (1 - m.3.ar.n1$coef[1])
#> intercept
#>   1.15698
# linear model
summary(m.3.lm.n1)$coefficients[1:3, 1:2]
#>                            Estimate  Std. Error
#> (Intercept)              0.9839341 0.053084123
#> log(dat$N1[1:(t - 1)])   0.9201864 0.009157214
#> log(dat$N2[1:(t - 1)]) -0.1443693 0.008777527
# Bayesian estimates
summary(m3.post.hmsc$Beta)$statistics[1:3, 1:2]
#>                                       Mean         SD
#> B[(Intercept) (C1), sp1 (S1)]   0.9829117 0.06723119
#> B[N1 (C2), sp1 (S1)]            0.9202360 0.01167056
#> B[N2 (C3), sp1 (S1)]           -0.1441626 0.01104150
```

```
# Simulate initial species population growth with environment fluctuations
N1.0 <- 10
N2.0 <- 10
r1.0 <- 1.7
r2.0 <- 1.7
alpha.11 <- 0.01
alpha.22 <- 0.01
alpha.12 <- 0.005
alpha.21 <- 0.01
# model function
disc_LV_comp <- function(r1, r2, N1.0, N2.0, alpha.11, alpha.22, alpha.12, alpha.21) {
```

```
    Nt1 <- (r1 * N1.0)/(1 + alpha.11 * N1.0 + alpha.12 * N2.0)
    Nt2 <- (r2 * N2.0)/(1 + alpha.22 * N2.0 + alpha.21 * N1.0)
    return(c(Nt1, Nt2))
}
# 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")
N$N1[1] <- N1.0
N$N2[1] <- N2.0
for (i in 2:t) {
    res <- disc_LV_comp(r1 = r1.0, r2 = r2.0, N1.0 = N[i - 1, 1], N2.0 = N[i - 1,
        2], alpha.11 = alpha.11, alpha.22 = alpha.22, alpha.12 = alpha.12, alpha.21 = alpha.21)
    N$N1[i] <- res[1]
    N$N2[i] <- res[2]
}
```

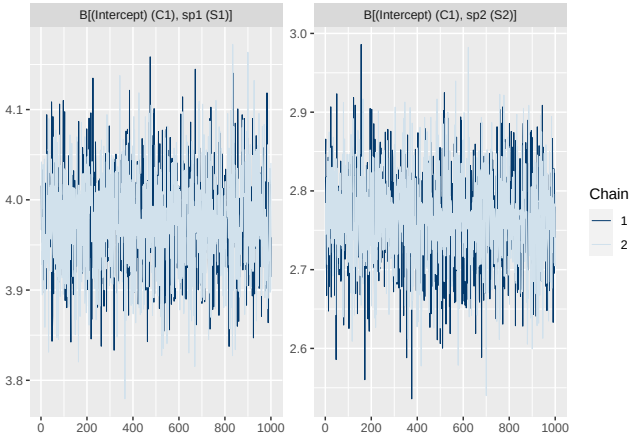
```
# Plot simulation: ggplot
N$time <- 1:t
dat <- melt(N, id.vars = "time")
ggplot2::ggplot(dat, aes(time, value, col = variable)) + geom_point() + geom_hline(yintercept = ((r1.0 -
    1)/alpha.11), linetype = "dashed", color = "gray")
```



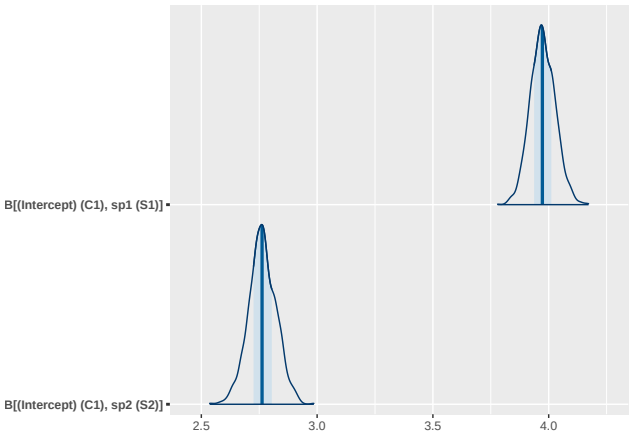

```
# Plot simulation: ggplot
dat <- as.data.frame(cbind(N$N1, N$N2))
colnames(dat) <- c("N1", "N2")
dat$time <- 1:t
df <- data.frame(cbind(log(dat$N1[2:t]), log(dat$N2[2:t])))
colnames(df) <- c("Nt1", "Nt2")
# prepare data in HMSC format
Y <- as.matrix(cbind(df$Nt1, df$Nt2))
XData <- data.frame(cbind(log(dat$N1[1:(t - 1)]), log(dat$N2[1:(t - 1)])))
studyDesign = data.frame(sample = as.factor(1:(t - 1)))
rL = HmscRandomLevel(units = studyDesign$sample)
m.4.hmsc = Hmsc(Y = Y, XData = XData, XFormula = ~1, studyDesign = studyDesign, ranLevels = list(sample
# Bayesian model parameters
nChains <- 2
```

```
thin <- 5
samples <- 1000
transient <- 500 * thin
verbose <- 500 * thin
# sample MCMC
m.4.sample <- sampleMcmc(m.4.hmsc, thin = thin, sample = samples, transient = transient,
    nChains = nChains, verbose = verbose)
#> Computing chain 1
#> Chain 1, iteration 2500 of 7500 (transient)
#> Chain 1, iteration 5000 of 7500 (sampling)
#> Chain 1, iteration 7500 of 7500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 7500 (transient)
#> Chain 2, iteration 5000 of 7500 (sampling)
#> Chain 2, iteration 7500 of 7500 (sampling)
```

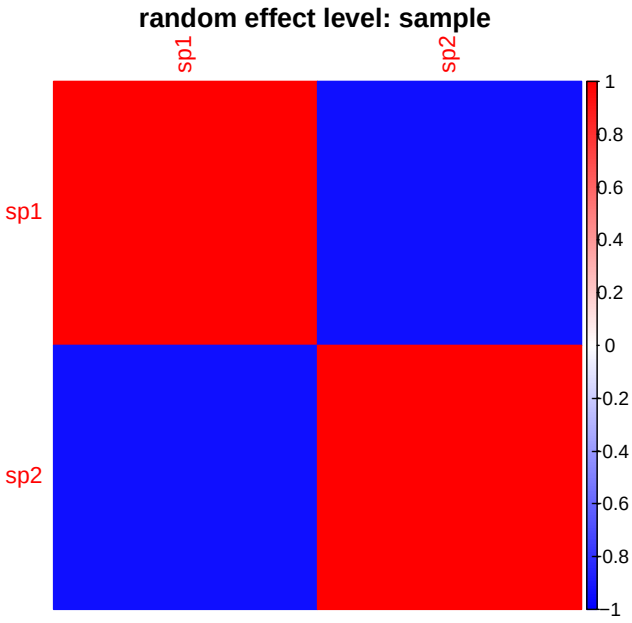
```
m4.post.hmsc <- convertToCodaObject(m.4.sample)
summary(m4.post.hmsc$Beta)
#>
#> Iterations = 2505:7500
#> Thinning interval = 5
#> Number of chains = 2
#> Sample size per chain = 1000
#>
#> 1. Empirical mean and standard deviation for each variable,
#>    plus standard error of the mean:
#>
#>                                  Mean      SD Naive SE Time-series SE
#> B[(Intercept) (C1), sp1 (S1)] 3.974 0.05406 0.001209       0.001173
#> B[(Intercept) (C1), sp2 (S2)] 2.764 0.06002 0.001342       0.001388
#>
#> 2. Quantiles for each variable:
#>
#>                                  2.5%   25%   50%   75% 97.5%
#> B[(Intercept) (C1), sp1 (S1)] 3.872 3.937 3.973 4.011 4.085
#> B[(Intercept) (C1), sp2 (S2)] 2.642 2.725 2.762 2.804 2.885
bayesplot::mcmc_trace(m4.post.hmsc$Beta)
```



```
bayesplot::mcmc_areas(m4.post.hmsc$Beta, area_method = c("equal height"))
```




```
OmegaCor = computeAssociations(m.4.sample)
supportLevel = 0.95
toPlot = ((OmegaCor[[1]]$support > supportLevel) + (OmegaCor[[1]]$support < (1 -
    supportLevel)) > 0) * OmegaCor[[1]]$mean
corrplot::corrplot(toPlot, method = "color", col = colorRampPalette(c("blue", "white",
    "red"))(200), title = paste("random effect level:", m.4.sample$rLNames[1]), mar = c(0,
    0, 1, 0))
```

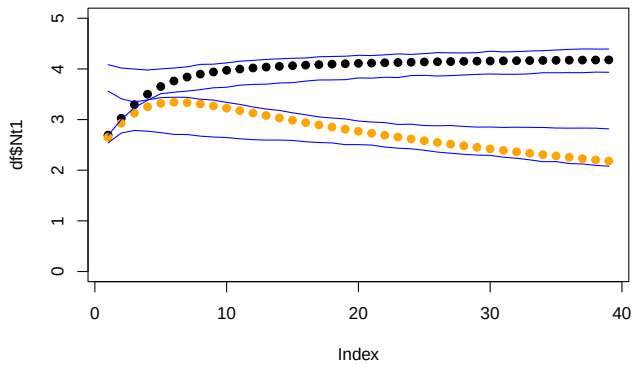


The HMSC model can estimate the species associations well.

```
# explanatory power
preds = computePredictedValues(m.4.sample)
# evaluateModelFit(hM = m.4.sample, predY = preds) predictive power /
# cross-validation partition = createPartition(m.4.sample, nfolds = 2) preds =
# computePredictedValues(m.4.sample, partition = partition, nParallel =
# nChains) evaluateModelFit(hM = m.4.sample, predY = preds) xx preds =
```

```
# computePredictedValues(m.4.sample, partition=partition, partition.sp=c(1,2),
# mcmcStep=10, nParallel = nChains) evaluateModelFit(hM=m.4.sample,
# predY=preds) xx etaPost=getPostEstimate(m.4.sample, 'Eta')
# lambdaPost=getPostEstimate(m.4.sample, 'Lambda') biPlot(m.4.sample, etaPost =
# etaPost, lambdaPost = lambdaPost, factors = c(1,2),'X1')
```

```
df$n1_25 <- NA
df$n1_975 <- NA
df$n2_25 <- NA
df$n2_975 <- NA
for (i in 1:39) {
    red <- preds[i, , ]
    a <- apply(red, 1, quantile, probs = c(0.025, 0.975))
    df$n1_25[i] <- a[1, 1]
    df$n1_975[i] <- a[2, 1]
    df$n2_25[i] <- a[1, 2]
    df$n2_975[i] <- a[2, 2]
}
plot(df$Nt1, pch = 19, col = "black", ylim = c(0, 5))
points(df$Nt2, pch = 19, col = "orange")
lines(df$n1_25, col = "blue")
lines(df$n1_975, col = "blue")
lines(df$n2_25, col = "blue")
lines(df$n2_975, col = "blue")
```



4 4 species growth, competition, with environmental change

The goal of the process was to use HMSC's latent variable approach to study the results of non-linear processes in ecology using a linear model. We can infer the direction and magnitude of the species interaction. We now consider an environmental covariate that changes over time and impacts each species growth. We will use HMSC from this point forward.

```
# Simulate initial species population growth with environment fluctuations
N1.0 <- 10
N2.0 <- 10
r1.0 <- 1.7
r2.0 <- 1.7
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

# model function
disc_LV_E <- function(r1, r2, N1.0, N2.0, alpha.11, alpha.22, alpha.12, alpha.21,
    E, x1, x2) {
    Nt1 <- ((r1 * exp(-(E - x1)^2)) * N1.0)/(1 + alpha.11 * N1.0 + alpha.12 * N2.0)
    Nt2 <- ((r2 * exp(-(E - x2)^2)) * N2.0)/(1 + alpha.22 * N2.0 + alpha.21 * N1.0)
    return(c(Nt1, Nt2))
}
# 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")
N$N1[1] <- N1.0
N$N2[1] <- N2.0
E <- rep(NA, t)
E[1] <- E.0
for (i in 2:t) {
    res <- disc_LV_E(r1 = r1.0, r2 = r2.0, N1.0 = N[i - 1, 1], N2.0 = N[i - 1, 2],
        alpha.11 = alpha.11, alpha.22 = alpha.22, alpha.12 = alpha.12, alpha.21 = alpha.21,
        E = E[i - 1], x1 = x1.0, x2 = x2.0)
    N$N1[i] <- res[1]
    N$N2[i] <- res[2]
    E[i] <- E[i - 1] + rnorm(1, 0, 0.1)
}
```

```
# 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 = ((r1.0 +
    1)/alpha.11), linetype = "dashed", color = "gray")
```

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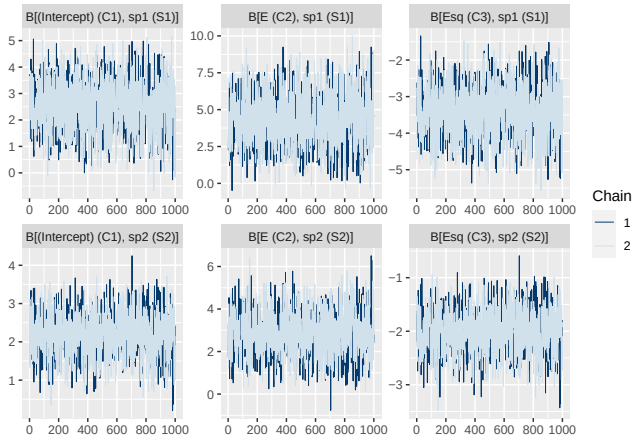
```
# Plot simulation: ggplot
dat <- as.data.frame(cbind(log(N$N1), log(N$N2)))
colnames(dat) <- c("N1", "N2")
dat$time <- 1:t
df <- data.frame(cbind(dat$N1[2:t], dat$N2[2:t]))
colnames(df) <- c("Nt1", "Nt2")
# prepare data in HMSC format
Y <- as.matrix(cbind(df$Nt1, df$Nt2))
XData <- data.frame(cbind(dat$N1[1:(t - 1)], dat$N2[1:(t - 1)]), E[1:(t - 1)], E[1:(t -
    1)]^2)
colnames(XData) <- c("n1", "n2", "E", "Esq")
studyDesign = data.frame(sample = as.factor(1:(t - 1)))
rL = HmscRandomLevel(units = studyDesign$sample)
m.5.hmsc = Hmsc(Y = Y, XData = XData, XFormula = ~E + Esq, studyDesign = studyDesign,
    ranLevels = list(sample = rL))
# Bayesian model parameters
nChains <- 2
thin <- 5
samples <- 1000
transient <- 500 * thin
verbose <- 500 * thin
# sample MCMC
m.5.sample <- sampleMcmc(m.5.hmsc, thin = thin, sample = samples, transient = transient,
    nChains = nChains, verbose = verbose)
#> Computing chain 1
#> Chain 1, iteration 2500 of 7500 (transient)
#> Chain 1, iteration 5000 of 7500 (sampling)
#> Chain 1, iteration 7500 of 7500 (sampling)
#> Computing chain 2
#> Chain 2, iteration 2500 of 7500 (transient)
#> Chain 2, iteration 5000 of 7500 (sampling)
#> Chain 2, iteration 7500 of 7500 (sampling)
```

```
m5.post.hmsc <- convertToCodaObject(m.5.sample)
summary(m5.post.hmsc$Beta)
#>
#> Iterations = 2505:7500
#> Thinning interval = 5
#> Number of chains = 2
#> Sample size per chain = 1000
#>
#> 1. Empirical mean and standard deviation for each variable,
#>    plus standard error of the mean:
#>
#>                                  Mean     SD Naive SE Time-series SE
#> B[(Intercept) (C1), sp1 (S1)]  2.572 0.9131 0.020417        0.02342
#> B[E (C2), sp1 (S1)]            4.274 1.6630 0.037186        0.04303
#> B[Esq (C3), sp1 (S1)]         -3.374 0.6726 0.015039        0.01740
#> B[(Intercept) (C1), sp2 (S2)]  2.204 0.5331 0.011920        0.01379
#> B[E (C2), sp2 (S2)]            2.832 0.9647 0.021571        0.02548
#> B[Esq (C3), sp2 (S2)]         -2.010 0.3893 0.008705        0.01037
#>
#> 2. Quantiles for each variable:
```

```
#>
#>                                    2.5%    25%    50%    75%  97.5%
#> B[(Intercept) (C1), sp1 (S1)]  0.6559  1.966  2.584  3.186  4.300
#> B[E (C2), sp1 (S1)]            1.1272  3.151  4.240  5.384  7.713
#> B[Esq (C3), sp1 (S1)]         -4.7501 -3.810 -3.367 -2.915 -2.088
#> B[(Intercept) (C1), sp2 (S2)]  1.1184  1.876  2.208  2.555  3.278
#> B[E (C2), sp2 (S2)]            0.8746  2.216  2.823  3.419  4.800
#> B[Esq (C3), sp2 (S2)]         -2.8112 -2.254 -2.009 -1.756 -1.235
bayesplot::mcmc_trace(m5.post.hmsc$Beta)
```



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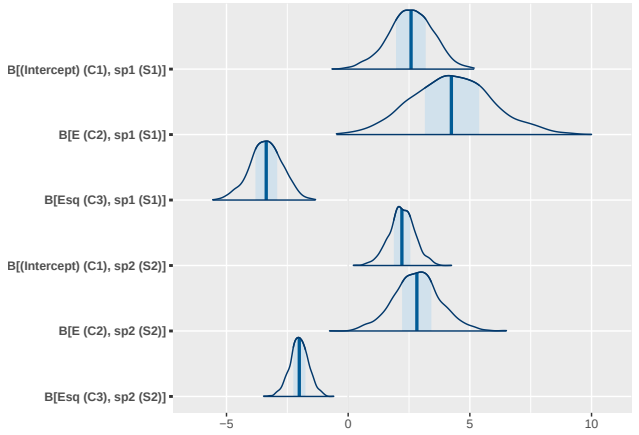
```
bayesplot::mcmc_areas(m5.post.hmsc$Beta, area_method = c("equal height"))
```



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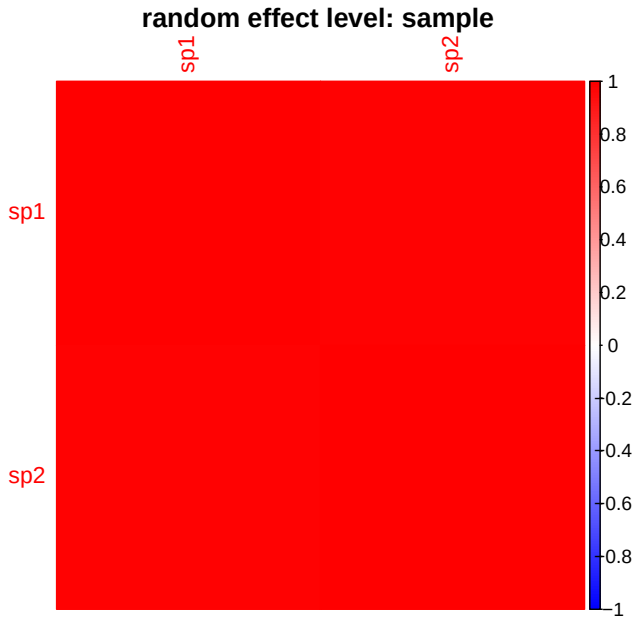
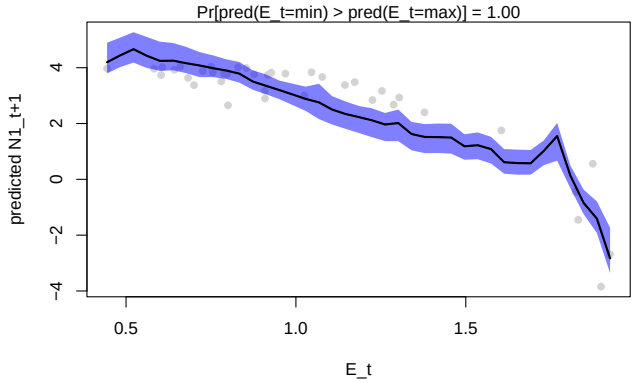
```
# Bayesian estimates
summary(m5.post.hmsc$Beta)$statistics[1:4, 1:2]
#>                                    Mean        SD
#> B[(Intercept) (C1), sp1 (S1)]  2.571888 0.9130903
#> B[E (C2), sp1 (S1)]            4.274430 1.6630073
#> B[Esq (C3), sp1 (S1)]         -3.373885 0.6725570
#> B[(Intercept) (C1), sp2 (S2)]  2.203589 0.5330636
```

```
OmegaCor = computeAssociations(m.5.sample)
supportLevel = 0.7
toPlot = ((OmegaCor[[1]]$support > supportLevel) + (OmegaCor[[1]]$support < (1 -
```

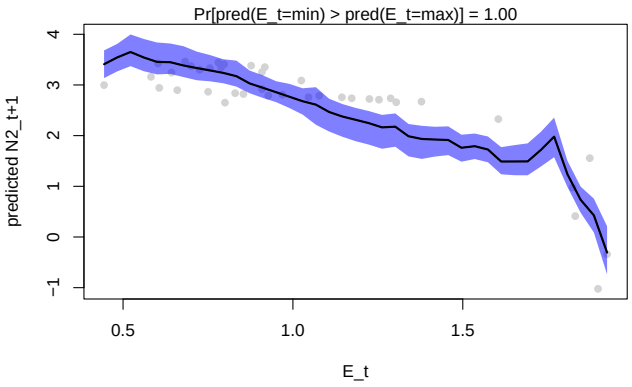
```
    supportLevel)) > 0) * OmegaCor[[1]]$mean
corrplot::corrplot(toPlot, method = "color", col = colorRampPalette(c("blue", "white",
    "red"))(200), title = paste("random effect level:", m.5.sample$rLNames[1]), mar = c(0,
    0, 1, 0))
```



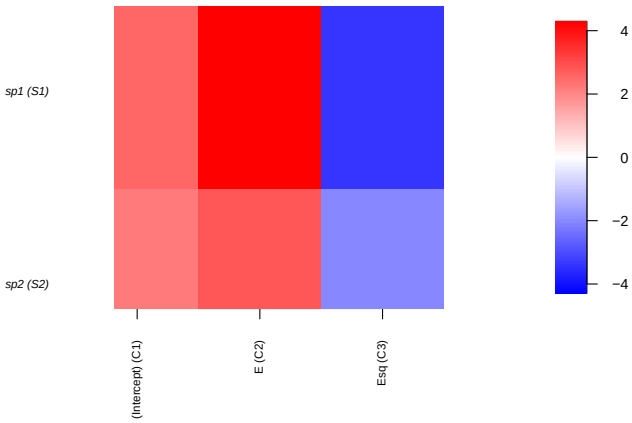

```
Gradient <- constructGradient(m.5.sample, focalVariable = "E", non.focalVariables = list(Esq = list(2))
    ngrid = 39)
predY <- predict(m.5.sample, XData = Gradient$XDataNew, expected = TRUE)
a <- plotGradient(m.5.sample, Gradient, pred = predY, showData = T, measure = "Y",
    index = 1, main = "", xlab = "E_t", ylab = "predicted N1_t+1")
```




```
b <- plotGradient(m.5.sample, Gradient, pred = predY, showData = T, measure = "Y",
    index = 2, main = "", xlab = "E_t", ylab = "predicted N2_t+1")
```




```
postBeta = getPostEstimate(m.5.sample, parName = "Beta")
plotBeta(m.5.sample, post = postBeta, param = "Mean", supportLevel = 0.7)
```



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References

Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations (Vol. 11). Springer Science & Business Media.

Certain, G., F. Barraquand, and A. Gårdmark. 2018. How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? Methods in Ecology and Evolution 9:1975–1995.

Erickson, K. D., and A. B. Smith. 2023. Modeling the rarest of the rare: A comparison between multi-species distribution models, ensembles of small models, and single-species models at extremely low sample sizes. Ecography 2023:e06500.

Hart, S. P., and D. J. Marshall. 2013. Environmental stress, facilitation, competition, and coexistence. Ecology 94:2719–2731.

Ingram, M., D. Vukcevic, and N. Golding. 2020. Multi-output gaussian processes for species distribution modelling. Methods in Ecology and Evolution 11:1587–1598.

Ives, A. R. 1995. Predicting the response of populations to environmental change. Ecology 76:926–941.

Kloppers, P. H., and J. C. Greeff. 2013. Lotka–volterra model parameter estimation using experiential data. Applied Mathematics and Computation 224:817–825.

Mühlbauer, L. K., M. Schulze, W. S. Harpole, and A. T. Clark. 2020. gauseR: Simple methods for fitting lotka-volterra models describing gause's "struggle for existence". Ecology and Evolution 10:13275–13283.

Olivença, D. V., J. D. Davis, and E. O. Voit. 2021. Comparison between lotka-volterra and multivariate autoregressive models of ecological interaction systems. bioRxiv.

133 Ovaskainen, O., G. Tikhonov, D. Dunson, V. Grøtan, S. Engen, B.-E. Sæther, and N. Abrego. 2017. How
134 are species interactions structured in species-rich communities? A new method for analysing time-series
135 data. Proceedings of the Royal Society B: Biological Sciences 284:20170768.