

model description

Justin Pomeranz

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Introduction

This model extends that of Zhou et al. 2013 which incorporates continuous predation and seasonal reproduction (typical life history of many aquatic organisms) of a 2-species predator-prey model.

We extend this model to include intraguild predation, in which a basal species B is consumed by two predators C, and P, where P (also called intraguild predator) can also consume C (also called intraguild prey).

Model overview

Assume there are habitat patches, x , located across a landscape. Within each patch, three species may exist. A basal species B, a consumer species C, and a predator species P. In the absence of predation, the basal species population abundance is assumed to grow exponentially to to some population level, K , (logistic growth) based on some characteristic of the habitat patch (i.e. environmental condition, patch size).

The consumer species (also know as the intraguild prey) receives all of its energy from the basal species. The consumer species population varies in direct proportion to the density of B, following a type II functional response (Holling's disk equation). The consumer species is also predated upon by the predator species, P.

The predator species consumes both B and C, and responds to each following a type II functional response.

Dispersal

The model starts with some initial nonzero population abundances for all three species in each patch. First, dispersal from all patches is accounted for. The number of emmigrants, E , for each species from each patch is estimated, Then, the number of emmigrants from patch i is divided into immigrants, I , for each patch j . The likelihood of an individual dispersal from patch i to j declines exponentially with increasing distance from patch i to j .

The probability that an individual disperses can be set with $p_{\text{dispersal}}$. A single value can be used for all trophic levels, or can be set for each individually.

Predation

After dispersal, continuous predation occurs. The number of prey i eaten by consumer j , W_{ij} , in a season is calculated as:

$$W_{ij} = \frac{\alpha_{ij} N_i N_j}{\beta_{ij} N_j + N_i}$$

where $N_{\{i\}}$ is the population abundance of resource i , $N_{\{j\}}$ is the population abundance of consumer j , and α_{ij} and β_{ij} are coefficients describing the functional response as the ratio of resources to consumers increases. β_{ij} describes how fast the predation curve reaches the asymptote of the type II functional response, and $\frac{\alpha}{\beta}$ determines the location of the asymptote.

The total number of Basal species individual eaten is the sum of the individuals eaten by C and P:

$$W_B = W_{BC} + W_{CP}$$

Survival

After accounting for predation, the remaining individuals are reduced by the base survival probability:

$$B' = S_0(B - W_B) \quad (1)$$

$$C' = S_0(C - W_{CP}) \quad (2)$$

$$P' = S_0P \quad (3)$$

Reproduction

Finally, those individuals remaining (X'_i) reproduce according to the following:

$$B_{t+1} = \frac{r_{max}}{1 + bB'} B' \quad (4)$$

$$C_{t+1} = \frac{e_{bc}\alpha_{bc}B}{\beta_{bc}C + B} C' \quad (5)$$

$$P_{t+1} = \left(\frac{e_{bp}\alpha_{bp}B}{\beta_{bp}P + B} + \frac{e_{bp}\alpha_{bp}C}{\beta_{bp}P + C} \right) P' \quad (6)$$

where r_{max} is the maximum per-capita reproduction rate of the basal species and $b = \frac{r_{max}-1}{K}$ determines the asymptotic relationship of population growth, where K is carrying capacity. In the absence of predation, population growth of the basal species follows a logistic growth relationship. Note the use of X_i in determining the predation effects (terms inside of the parentheses) and X'_i to estimate reproduction in the next generation. This can be viewed as a time lag, which incorporates continuous predation through the season, and synchronous reproduction only for the surviving individuals.

For the consumer species (C and P) the product of $e_{ij}\alpha_{ij}$ is the maximum reproductive rate of consumer j on resource i . The carrying capacity of consumer j on resource i is $\frac{N_i(e_{ij}\alpha_{ij}-1)}{\beta_{ij}}$ when $N_{\{i\}}$ is constant

Time $t + 1$

To ensure that the number of individuals in time $t + 1$ is an integer and to include stochasticity in our model, the population abundance for $t + 1$ is drawn from a Poisson distribution:

$$X_i \sim \text{Poisson}(\lambda_i)$$

where

$$\lambda_i = B_{t+1}, C_{t+1}, P_{t+1}$$

Disturbance

We also include a disturbance probability $p_{disturbance}$ which reduces the abundance of each species present in patch x at time i by some constant value (e.g., if disturbance occurs, populations are reduced by 50%).

Disturbance correlation. The correlation value can be set such that if one patch undergoes a disturbance as described above, then patches located nearby (euclidean distance, same branch, etc.) are also more likely to undergo that disturbance. This can be viewed as a flood disturbance through a river branch, or a large storm even across a 2-dimensional landscape.

Resource extinction

An explicit assumption of our model is that the presence of a consumer is dependent on the presence of at least one of its' resources. Therefore, if the population abundance of B is equal to 0 at the beginning of a timestep, we force the abundances of C and P to also equal zero. Note that C and P can become locally extinct and the simulation will continue as normal, and any secondary extinctions are the direct result of trophic dynamics.

food chain length

There are 5 possible outcomes, and their corresponding food chain lengths

- all species are extinct FCL = 0
- B present FCL = 1
- $B + C$ FCL = 2
- $B + P$ FCL = 2.5
- $B + C + P$ FCL = 3

Environment

The carrying capacity, K , is a function which is determined by ecosystem area (i.e., number of patches upstream) or some environmental condition. If determined by environmental condition, patches can either be randomly assigned a value, or can be spatially auto-correlated, such that nearby patches are more likely to have similar environmental values.

Simulation function `igp_sim()`

The main function is `igp_sim()`, which simulates trophic dynamics between three species in patches. By default, the species are classified as basal B , consumer C , and predator P .

A distance matrix describing how patches are oriented spatially can be included with the `dist_mat` argument, or otherwise patches are assumed to be randomly distributed in a 10x10 square.

Carrying capacity of the basal species can be determined by the `k` argument. If one value is supplied, it is assumed that carrying capacity is the same for all patches. You can set `k` for each patch individually with a vector of length = `n_patch` in the `k` argument. In the **future**, a function will be implemented to calculate carrying capacity based on number of patches upstream, or randomly across all patches (possibly other implementations). `r_max` controls the maximum reproduction rate for the basal species, B .

The probability that an individual will disperse from a patch is set with the `p_dispersal` argument, and can take values from 0 to 1. If one value is supplied it is applied to all three species, otherwise a vector of length 3 can be used to set probabilities for species B , C and P (in that order). The `theta` argument

determines how quickly dispersal ability declines with increasing distance (higher values of **theta** means individuals will disperse shorter distances). Currently, only one value of theta is applied to all three species.

Trophic dynamics are determined with the arguments **e{ij}**, **alpha{ij}** and **beta{ij}**, where *{ij}* describes the relationship between resource *i* and consumer *j*. **e{ij}** refers to the conversion efficiency, and **alpha{ij}** and **beta{ij}** are parameters controlling the type II functional response.

The **s0** argument controls the base survival probability. Currently it sets the same survival probability for all species.

The **p_disturb** argument sets the probability that any given patch experiences a disturbance in a given time step. This value should be set very low (i.e., 1e-4) due to the high number of rolls in a given simulation **n_patch * t**. The **mag_disturb** argument controls the strength of disturbance, and reduces the population of all species to that value. i.e. **mag_disturb = 0.25** reduces the population to 25%.

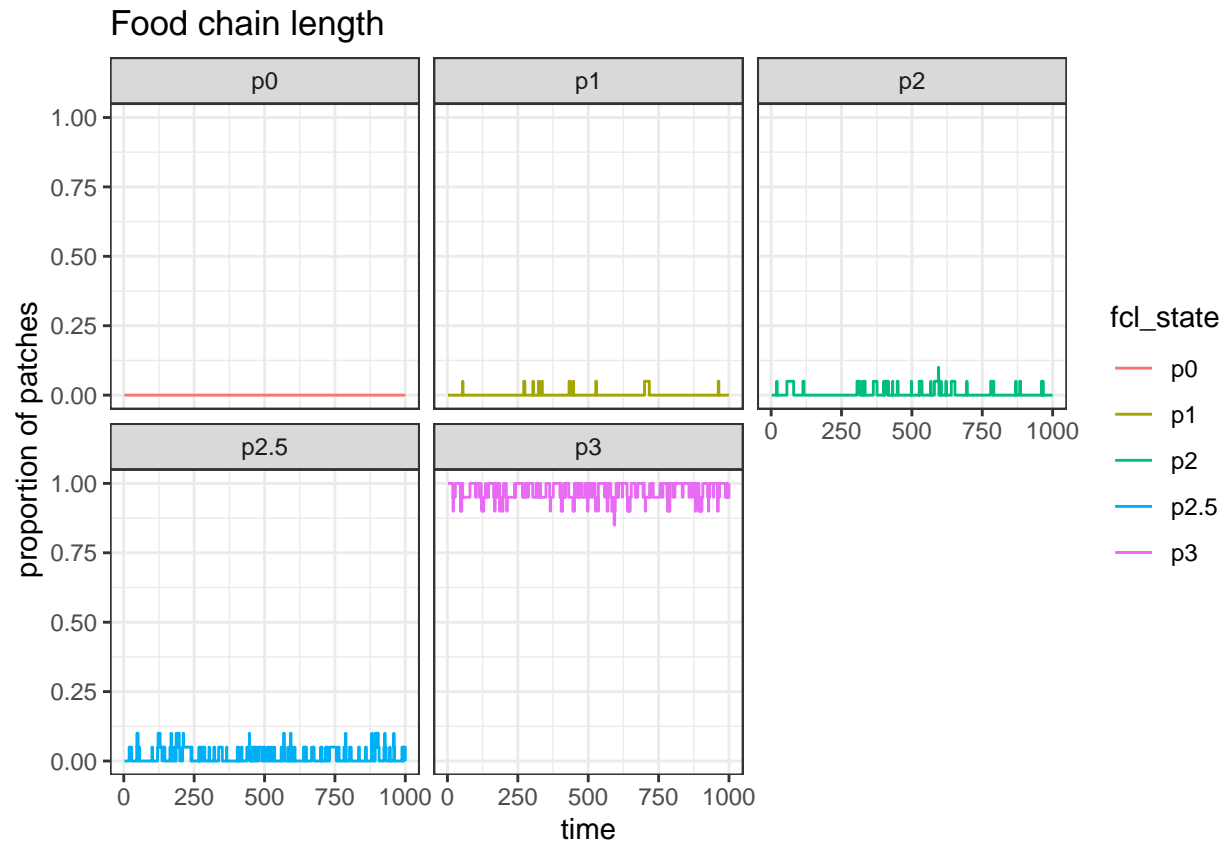
t controls the number of timesteps to run the simulation for.

The **plot_{descriptor}** arguments control which plots will be displayed.

Proportion of patches with food chain length *S* at each time step:

```
d <- igp_sim(p_disturb = 0.01,
            alphabp = 10,
            plot_disturbance = FALSE,
            plot_fcl = TRUE,
            plot_patch_dynamics = FALSE)
```

```
## [1] "No distance matrix supplied, assuming 10x10 square landscape"
## [1] "only one value of k supplied, assuming it is the same in all patches"
```

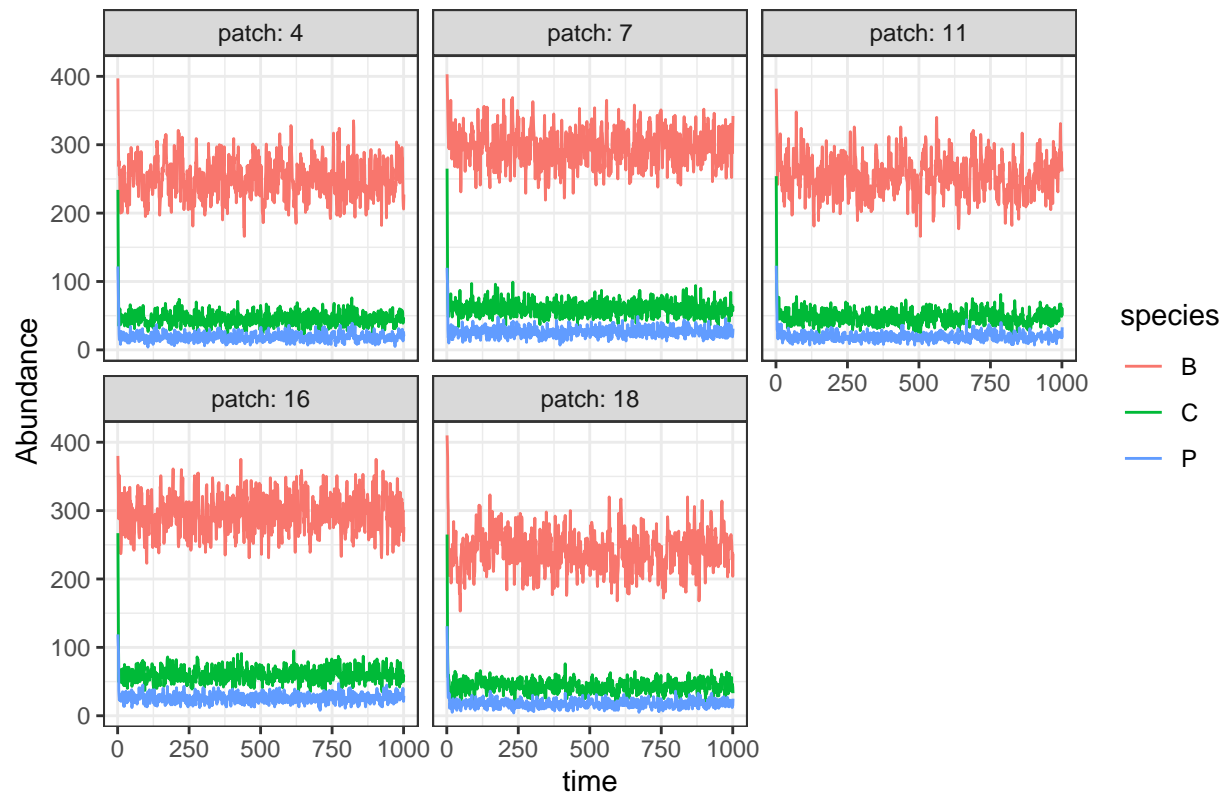


Dynamics of 5 random patches

```
d <- igp_sim(plot_disturbance = FALSE,
             plot_fcl = FALSE,
             plot_patch_dynamics = TRUE)
```

```
## [1] "No distance matrix supplied, assuming 10x10 square landscape"
## [1] "only one value of k supplied, assuming it is the same in all patches"
```

Dynamics for 5 random patches

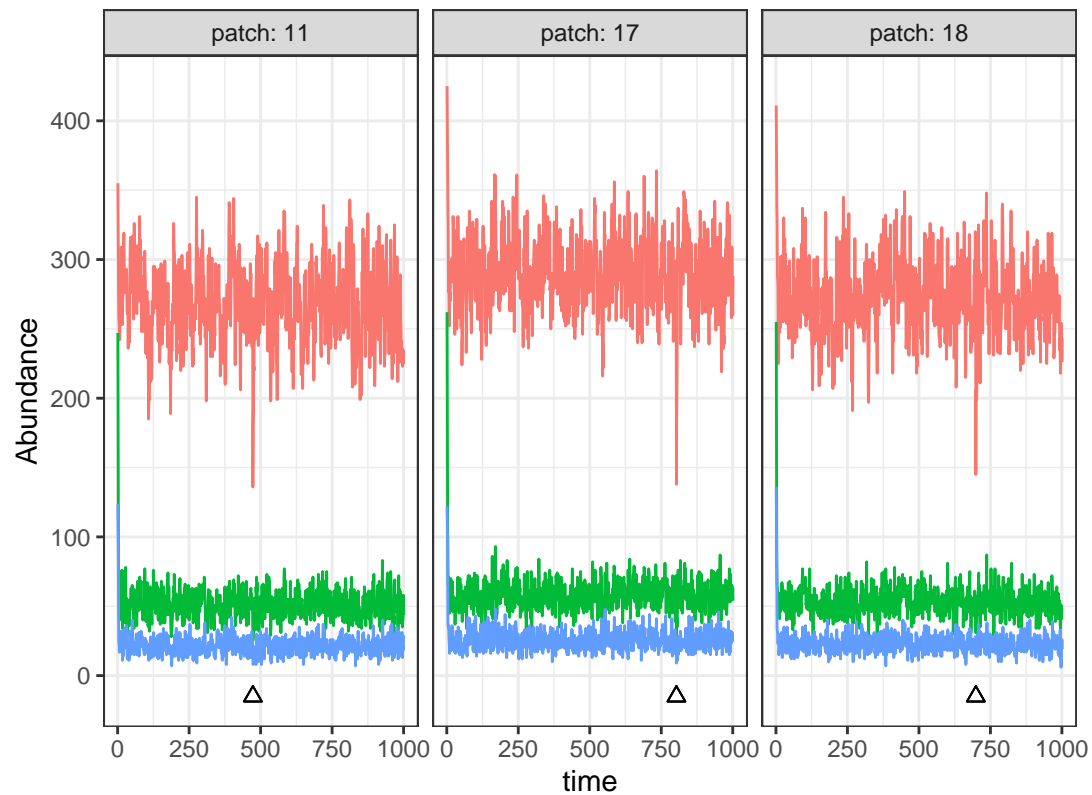


dynamics of all patches which experienced a disturbance: (if no disturbances occur, currently throws an error. Maybe remove this from main function and add it as a separate function to run on the output of `igp_sim()`?)

```
set.seed(001) # to ensure that at least one disturbance occurs
d <- igp_sim(plot_disturbance = TRUE,
             plot_fcl = FALSE,
             plot_patch_dynamics = FALSE)
```

```
## [1] "No distance matrix supplied, assuming 10x10 square landscape"
## [1] "only one value of k supplied, assuming it is the same in all patches"
```

All patches experiencing disturbances



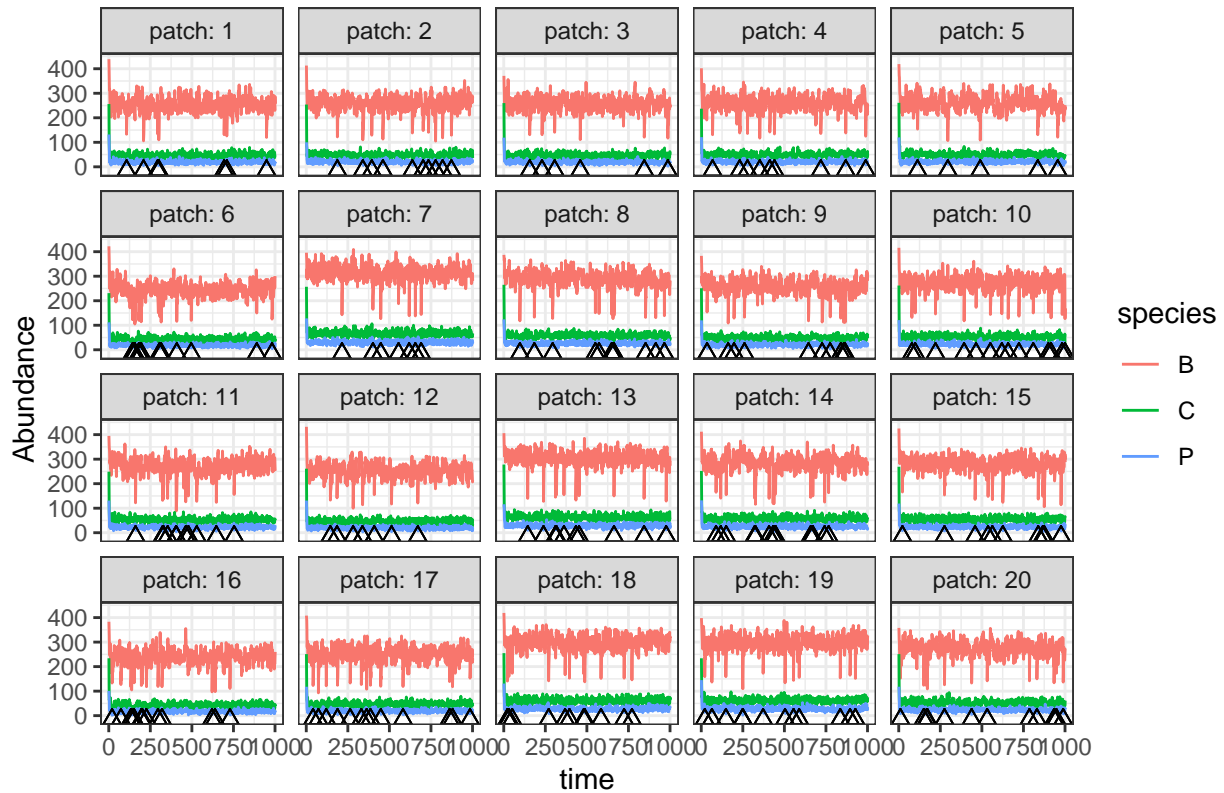
When a disturbance occurs at time step = t , it is displayed with a triangle below the x axis.

Increasing the frequency of disturbance makes this clear:

```
d <- igp_sim(p_disturb = 0.01,
             plot_disturbance = TRUE,
             plot_fcl = FALSE,
             plot_patch_dynamics = FALSE)
```

```
## [1] "No distance matrix supplied, assuming 10x10 square landscape"
## [1] "only one value of k supplied, assuming it is the same in all patches"
```

All patches experiencing disturbances

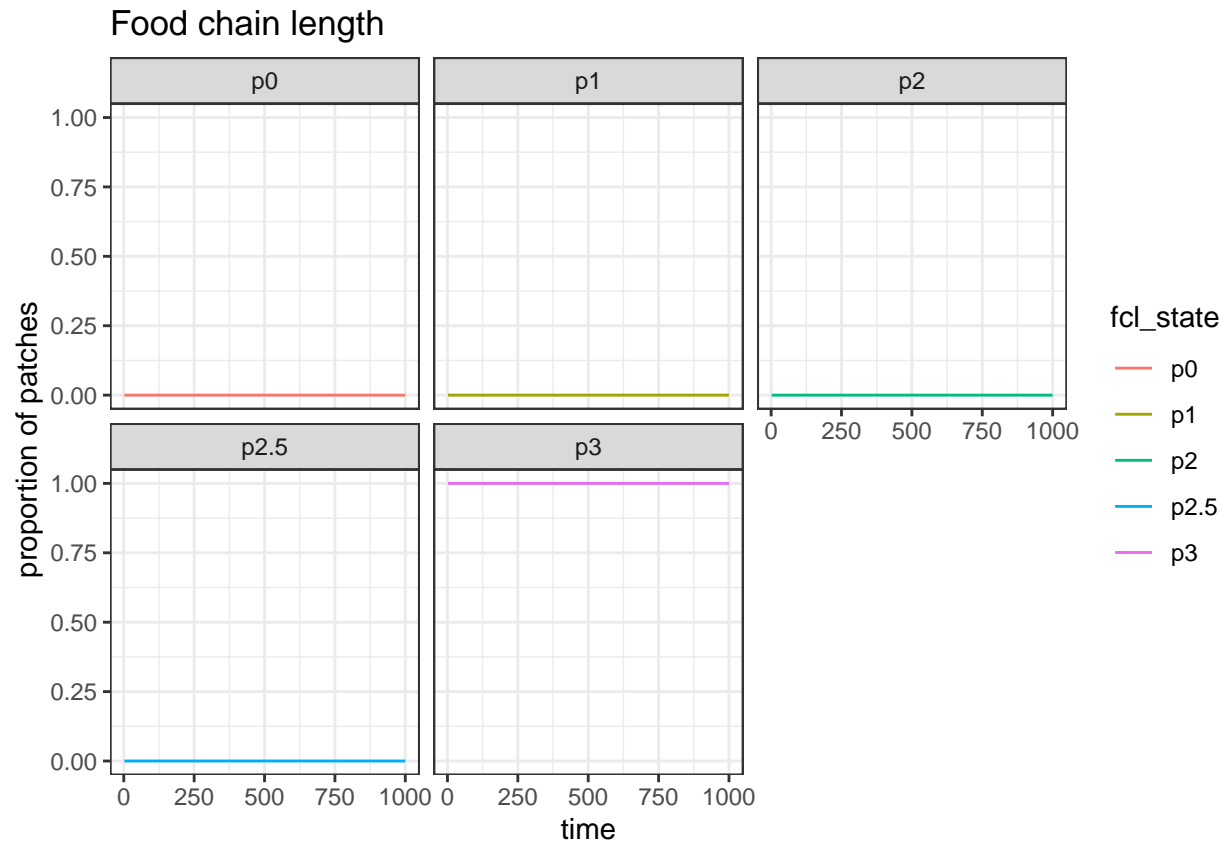


Customize settings

The arguments controlling the trophic dynamics are currently set to maximize stability and coexistence of all three species (parameter values based on the results of Zhou et al. 2013). This can be seen if we turn off dispersal and reduce disturbance probability

```
set.seed(1222) # for reproducibility
d <- igp_sim(n_patch = 100,
             p_dispersal = 0,
             mag_disturb = 1, # disturbance does not reduce population
             plot_disturbance = FALSE,
             plot_patch_dynamics = FALSE)
```

```
## [1] "No distance matrix supplied, assuming 10x10 square landscape"
## [1] "only one value of k supplied, assuming it is the same in all patches"
```

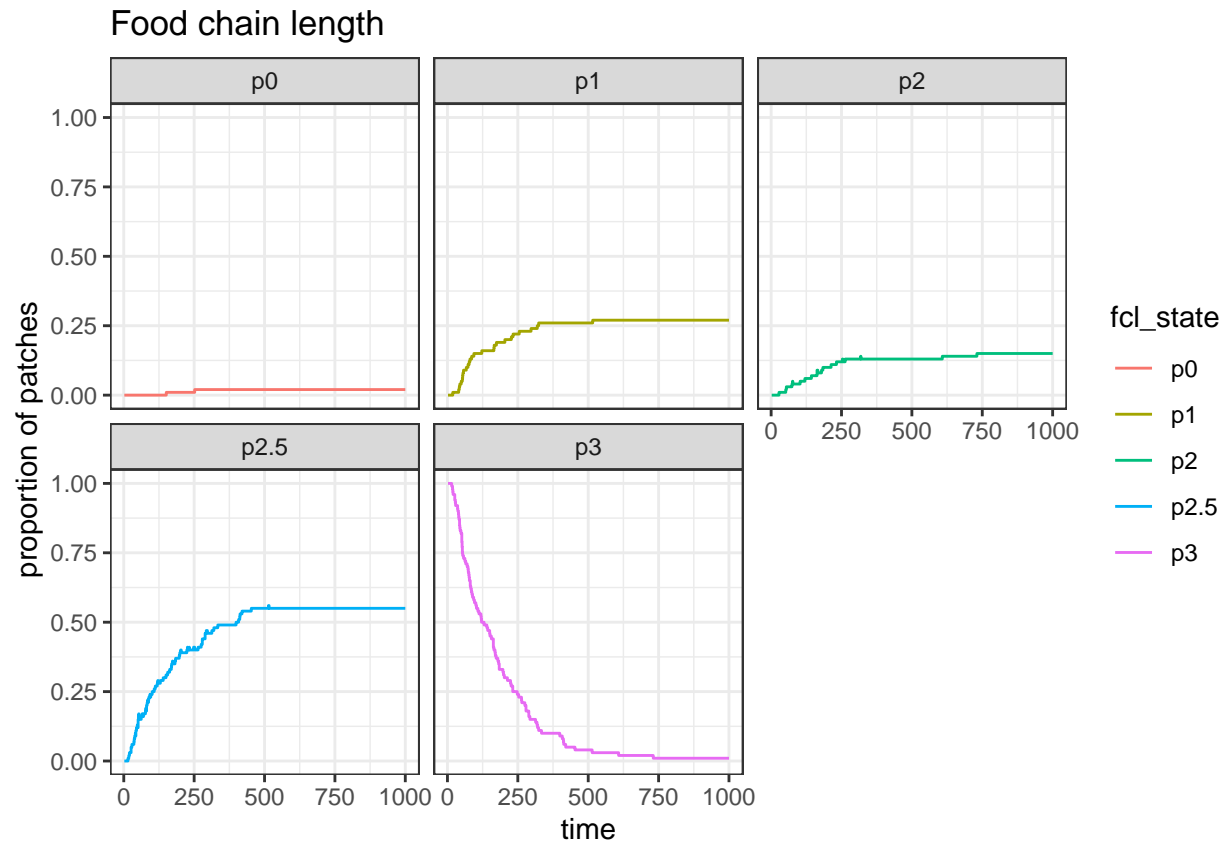



As we can see, the proportion of patches with FCL_state = 3 (all species present) is 100%.

Keeping dispersal and disturbance low, we can modify the strength of the trophic dynamics. A key point that increases stability, is ensuring that C out competes P for their shared resource (weak IGP). We can increase probability of extinction if we make P a stronger competitor

```
set.seed(1222) # for reproducibility
d <- igp_sim(n_patch = 100,
  p_dispersal = 0,
  mag_disturb = 1, # disturbance does not reduce population
  alphabp = 10,
  plot_disturbance = FALSE,
  plot_patch_dynamics = FALSE)
```

```
## [1] "No distance matrix supplied, assuming 10x10 square landscape"
## [1] "only one value of k supplied, assuming it is the same in all patches"
```

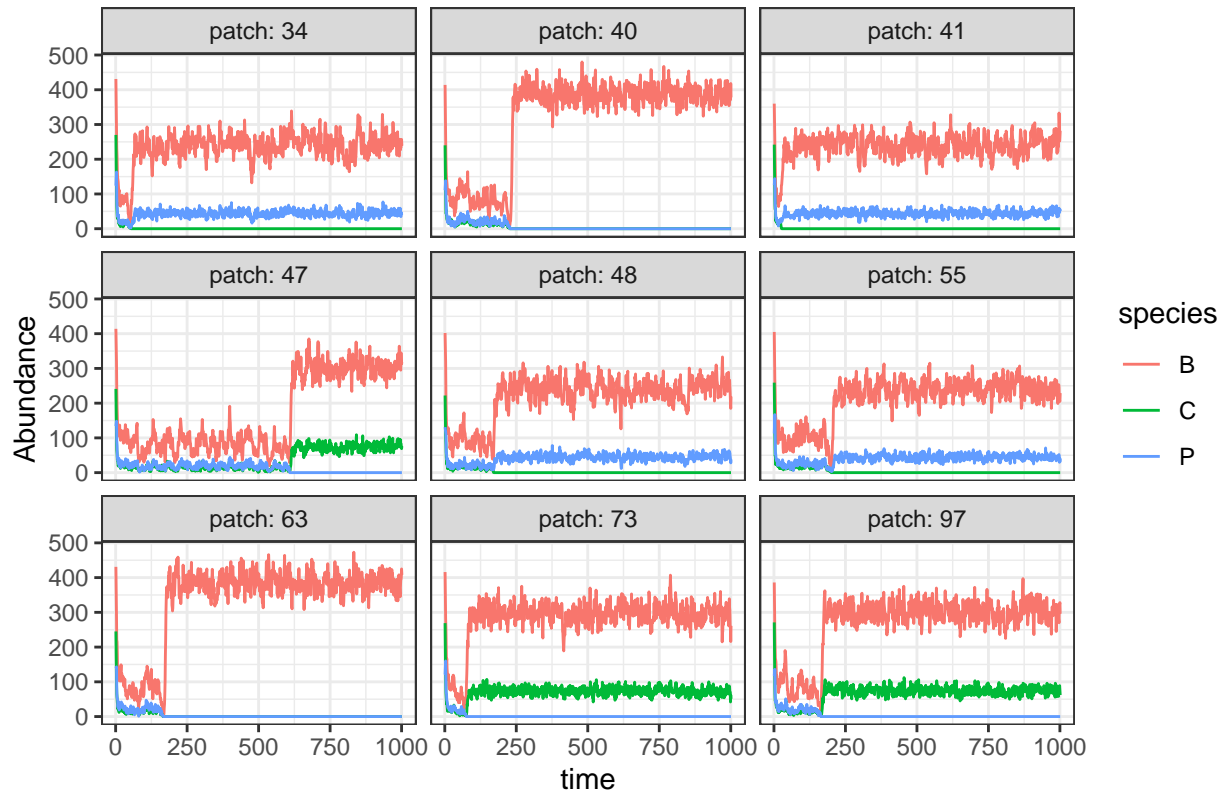


FCL_state = 2.5 → has species B and P, and C is removed.

Plot of patch dynamics for 9 random patches:

```
set.seed(122)
d$sp_dynamics %>%
  filter(patch %in% sample(1:100, 9)) %>%
  ggplot(
    aes(y = value,
        x = time,
        color = species)) +
  geom_line() +
  facet_wrap(~patch, labeller = label_both) +
  labs(y = "Abundance",
       title = "Dynamics for 5 random patches") +
  theme_bw() +
  NULL
```

Dynamics for 5 random patches



Here we can see that the green species (C) often goes extinct, and the blue species (P) also sometimes goes extinct.