Case Study 1: Bogdan et al. 2020

Two versions of a simple model

The first case study in this manuscript creates a model for *Carpobrotus spp.* It is a simple IPM (i.e. no discrete states, one continuous state variable). The data that the regressions are fit to are included in the `ipmr` package, and can be accessed with `data(iceplant_ex)`.

The IPM can be written on paper as follows:

1. $n(z', t+1) = \int_L^U K(z', z) n(z, t) dz$
2. $K(z', z) = P(z', z) + F(z', z)$
3. $P(z', z) = S(z) * G(z', z)$
4. $F(z', z) = p_f(z) * f_s(z) * p_r * f_d(z')$

The components of each sub-kernel are either regression models or constants. Their functional forms are given below:

5. $Logit^{-1}(S(z)) = \alpha_s + \beta_s * z$
6. $G(z', z) \sim Norm(\mu_g, \sigma_g)$
7. $\mu_g = \alpha_g + \beta_g * z$
8. $Logit^{-1}(p_f(z)) = \alpha_{p_f} + \beta_{p_f} * z$
9. $Log(f_s(z)) = \alpha_{f_s} + \beta_{f_s} * z$
10. $f_d(z') \sim Norm(\mu_{f_d}, \sigma_{f_d})$

αs and βs correspond to intercepts and slopes from regression models, respectively. The other parameters are constants derived directly from the data itself.

```
library(ipmr)

data(iceplant_ex)

# growth model.

grow_mod <- lm(log_size_next ~ log_size, data = iceplant_ex)
grow_sd  <- sd(resid(grow_mod))

# survival model

surv_mod <- glm(survival ~ log_size, data = iceplant_ex, family = binomial())

# Pr(flowering) model

repr_mod <- glm(repro ~ log_size, data = iceplant_ex, family = binomial())

# Number of flowers per plant model
```

```r
flow_mod <- glm(flower_n ~ log_size, data = iceplant_ex, family = poisson())

# New recruits have no size(t), but do have size(t + 1)

recr_data <- subset(iceplant_ex, is.na(log_size))

recr_mu  <- mean(recr_data$log_size_next)
recr_sd  <- sd(recr_data$log_size_next)

# This data set doesn't include information on germination and establishment.
# Thus, we'll compute the realized recruitment parameter as the number
# of observed recruits divided by the number of flowers produced in the prior
# year.

recr_n   <- length(recr_data$log_size_next)

flow_n   <- sum(iceplant_ex$flower_n, na.rm = TRUE)

recr_pr  <- recr_n / flow_n


# Now, we put all parameters into a list. This case study shows how to use
# the mathematical notation, as well as how to use predict() methods

all_params <- list(
  surv_int = coef(surv_mod)[1],
  surv_slo = coef(surv_mod)[2],
  repr_int = coef(repr_mod)[1],
  grow_int = coef(grow_mod)[1],
  grow_slo = coef(grow_mod)[2],
  grow_sdv = grow_sd,
  repr_slo = coef(repr_mod)[2],
  flow_int = coef(flow_mod)[1],
  flow_slo = coef(flow_mod)[2],
  recr_n   = recr_n,
  flow_n   = flow_n,
  recr_mu  = recr_mu,
  recr_sd  = recr_sd,
  recr_pr  = recr_pr
)
```

The next chunk generates a couple constants used to implement the model. We add 20% to the smallest and largest observed sizes to minimize eviction, and will implement the model with 100 meshpoints.

```r
L <- min(c(iceplant_ex$log_size,
           iceplant_ex$log_size_next),
         na.rm = TRUE) * 1.2

U <- max(c(iceplant_ex$log_size,
           iceplant_ex$log_size_next),
         na.rm = TRUE) * 1.2

n_mesh_p <- 100
```

We now have the parameter set prepared, and have the boundaries for our domains set up. We are ready to implement the model. We'll specify `return_main_env = TRUE` in `make_ipm()` because we'll need the mesh points and bin width for some subsequent analyses.

We start with the function `init_ipm()`. This function has two arguments: `model_class` and `has_age`. For now, we will ignore the latter argument, as it is covered in case study 2, and has its own introduction here. The `model_class` argument specifies the type of IPM we are building and has 3 parts:

1. `simple/general`: This determines whether the model is a simple IPM or a general IPM.
2. `di/dd`: This determines whether the model is density independent (`di`) or density dependent (`dd`). Density dependent models aren't yet implemented, but will hopefully be implemented soon.
3. `det/stoch`: This determines whether the model is deterministic (`det`) or stochastic (`stoch`). This particular model is deterministic, as there are no data on temporal or spatial changes in vital rates. An introduction to stochastic models is available here.

Once we've decided on the type of model we want, we create the model class by specifying a string with each component separated by underscores (`"_"`). This case study is a simple, density independent, deterministic IPM, so the `model_class = "simple_di_det"`.

```
carpobrotus_ipm <- init_ipm('simple_di_det')
```

After we have initialized our IPM, we need to start adding sub-kernels using the `define_kernel()` function. These correspond to equations 3 and 4 above. We'll start with the `P` kernel. It contains functions that describe survival of individual ramets, and, if they survive, their new sizes.

1. Survival is modeled with a logistic regression to predict the probability of survival to $t+1$ based on the size of the ramet at t (`surv_mod`). In order to use the coefficients from that model to generate a survival probability, we need to know the inverse logit transformation, or, a function that performs it for us based on the linear predictor.
2. Size at $t+1$ is modeled with a Gaussian distribution with two parameters: the mean and standard deviation from the mean. The mean value of size at $t+1$ (`mu_g`) is itself a linear function of size at t and is parameterized with coefficients from the linear model (`grow_mod`). The standard deviation is a constant derived from the residual variance from the linear model we fit.

We start providing information on the `P` kernel by giving it a `name`. The name is important because we can use it to reference this kernel in higher level expression later on. It can have any name we want, but `P` is short, sweet, and consistent with the literature in this field (e.g. Easterling, Ellner & Dixon 2000, Ellner & Rees 2006). Next, we write the `formula`. The `formula` is the form of the kernel, and should look like Equation 3, minus the zs and z's.

```
carpobrotus_ipm <-  define_kernel(
  proto_ipm = carpobrotus_ipm,
  name      = "P",
  formula   = S * G
)
```

The `family` comes after formula. It describes the type of transition the kernel is implementing. `family` can be one of 4 options:

1. `"CC"`: Continuous state -> continuous state.
2. `"DC"`: discrete state -> continuous state.
3. `"CD"`: continuous state -> discrete state.
4. `"DD"`: discrete state -> discrete state.

Since this is a simple IPM with only 1 continuous state variable and 0 discrete state variables, the `family` will always be `"CC"`. In general IPMs, this will not always be true.

```
carpobrotus_ipm <-  define_kernel(
  proto_ipm = carpobrotus_ipm,
  name      = "P",
  formula   = S * G,
  family    = "CC"
)
```

We've now reached the `...` section of `define_kernel()`. The `...` part takes a set of named expressions that represent the vital rate functions we described in equations 5-7 above. The names on the left hand side of the `=` should appear either in the `formula` argument, or in other parts of the `....` The expressions on the right hand side should generate the values that we want to plug in. For example, Equation 5 ($Logit^{-1}(S(z)) = \alpha_s + \beta_s * z$) makes use of the `plogis` function in the `stats` package to compute the survival probabilities from our linear model. The names of the coefficients match the names in the `all_params` object we generated above. Another thing to note is the use of `z_1` and `z_2`. These are place-holders for z, z' in the equations above. `ipmr` will generate values for these internally using information that we provide in some of the next steps.

```
carpobrotus_ipm <-  define_kernel(
  proto_ipm = carpobrotus_ipm,
  name      = "P",
  formula   = S * G,
  family    = "CC",
  G         = dnorm(z_2, mu_g, grow_sdv),
  mu_g      = grow_int + grow_slo * z_1,
  S         = plogis(surv_int + surv_slo * z_1)
)
```

After setting up our vital rate functions, the next step is to provide a couple more kernel-specific details:

1. `data_list`: this is the `all_params` object we created above. It contains the names and values of all the constants in our model.
2. `states`: A list that contains the names of the state variables in the kernel. In our case, we've just called them `"z"`. The `states` argument controls the names of the variables `z_1` and `z_2` that are generated internally. We could just as easily call them something else - we would just have to change the vital rate expressions to use those names instead. For example, in this model, z, z' is the log-transformed surface area of ramets. We could abbreviate that with `"log_sa"`. In that case, `z_1,z_2` would become `log_sa_1, log_sa_2` in the vital rate expressions.
3. `evict_cor`: Whether or not to correct for eviction (Williams et al. 2012).
4. `evict_fun`: If we decide to correct for eviction, then a function that will correct it. In this example, we use `ipmr`'s `truncated_distributions` function. It takes two arguments: `fun`, which is the abbreviated form of the probability function family (e.g. "norm" for Gaussian, "lnorm" for log-normal, etc.), and `param`, which is the name in `...` that it modifies.

```
carpobrotus_ipm <-  define_kernel(
  proto_ipm = carpobrotus_ipm,
  name      = "P",
  formula   = S * G,
  family    = "CC",
  G         = dnorm(z_2, mu_g, grow_sdv),
  mu_g      = grow_int + grow_slo * z_1,
  S         = plogis(surv_int + surv_slo * z_1),
  data_list = all_params,
  states    = list(c("z")),
  evict_cor = TRUE,
  evict_fun = truncated_distributions(fun   = "norm",
```

```
                                        param = "G")
)
```

We've now defined our first sub-kernel! The next step is to repeat this process for the `F` kernel, which is Equations 4 and 8-10.

```
carpobrotus_ipm <-  define_kernel(
  proto_ipm = carpobrotus_ipm,
  name      = "F",
  formula   = recr_pr * f_s * f_d * p_f,
  family    = "CC",
  f_s       = exp(flow_int + flow_slo * z_1),
  f_d       = dnorm(z_2, recr_mu, recr_sd),
  p_f       = plogis(repr_int + repr_slo * z_1),
  data_list = all_params,
  states    = list(c("z")),
  evict_cor = TRUE,
  evict_fun = truncated_distributions(fun   = "norm",
                                      param = "f_d")
)
```

We've defined our sub-kernels. We are now ready to define the projection kernel, $K(z', z)$ and the model iteration procedure (Equations 1-2). We'll use the `define_k()` function instead of `define_kernel()`. The key difference between `define_k()` and `define_kernel()` is that the former does not have a `formula` argument. Rather, it just uses `...` to specify the form of the projection kernel and iteration procedures. Additionally, the family argument is now `"IPM"` rather than one of the other 4 described above.

Here, we encounter two more variablest that `ipmr` generates internally: `n_z_t_1` and `n_z_t`. These are placeholders for the population trait distribution functions. As above, we could call them anything else we want and just change the list in the `states` argument. We don't correct for eviction here because we have already done so in the sub-kernels.

```
carpobrotus_ipm <- define_k(
  proto_ipm = carpobrotus_ipm,
  name      = "K",
  family    = "IPM",
  K         = P + F,
  n_z_t_1   = K %*% n_z_t,
  data_list = all_params,
  states    = list(c('z')),
  evict_cor = FALSE
)
```

We have now defined the mathematical form of the IPM. The next step is tell `ipmr` how to implement it numerically. To do this, we use `define_impl()`, `define_domains()`, and `define_pop_state()`.

The first function tells `ipmr` which integration rule to use, which domain to start on, and which domain to end on for every kernel in the model. The format of the list it takes in the `kernel_impl_list` argument can be tricky to implement right, so the helper function `make_impl_args_list()` makes sure everything is formatted properly. The `kernel_names` argument can be in any order. The `int_rule`, `dom_start`, and `dom_end` arguments are then matched to kernels in the `proto_ipm` based on the order in the `kernel_names`. Note that, at the moment, the only integration rule that's implemented is `"midpoint"`. `"trapezoid"` and `"gauss_legendre"` are in the works, and others can be implemented by popular demand.

```
carpobrotus_ipm <-  define_impl(
  proto_ipm = carpobrotus_ipm,
  make_impl_args_list(
```

```
    kernel_names = c("K", "P", "F"),
    int_rule     = rep('midpoint', 3),
    dom_start    = rep('z', 3),
    dom_end      = rep('z', 3)
  )
)
```

Next, we define the range of values that our state variable, z/`z` can take on. This is done using `define_domains`. The `...` argument should have named vectors. The name should match the name of the `state`/`domain`. The first value in the vector is lower boundary, the second entry is the upper boundary, and the third entry is the number of bins to divide that range into.

```
carpobrotus_ipm <-  define_domains(
  proto_ipm = carpobrotus_ipm,
  z         = c(L, U, n_mesh_p)
)
```

Finally, we define the initial population state. In this case, we just use a uniform vector, but we could also use custom functions we defined on our own, or pre-specified vectors. The name of the population vector should be the name of the `state`/`domain`, with an `"n_"` attached to the front.

```
carpobrotus_ipm <-  define_pop_state(
  proto_ipm = carpobrotus_ipm,
    n_z     = rep(1/100, n_mesh_p)
)
```

IUp until this point, all we've done is add components to the `proto_ipm`. We now have enough information in it to build a model, iterate it, and compute some basic quantities. We'll set `return_main_env = TRUE` because we need the meshpoints and bin width for the analyses we'll do in the Further Analyses section.

```
carpobrotus_ipm <-  make_ipm(
  proto_ipm       = carpobrotus_ipm,
  iterate         = TRUE,
  iterations      = 100,
  return_main_env = TRUE
)


asymp_grow_rate <- lambda(carpobrotus_ipm)
asymp_grow_rate
```

```
## [1] 0.9759257
```

We see that the population is projected to shrink slightly. Next, we'll go through an alternative implementation of the model using `predict(surv_mod)` instead of the mathematical form of the linear predictors. After that, we'll explore a couple additional analyses to see what is going on with this population of iceplants.

Using predict methods instead

We can simplify the code a bit more and get rid of the mathematical expressions for each regression model's link function by using `predict()` methods instead. The next chunk shows how to do this. Instead of extracting parameter values, we put the model objects themselves into the `data_list`. Next, we specify the `newdata` object where the name corresponds to the variable name(s) used in the model in question, and the values are the domain you want to evaluate the model on.

Above, we added parts to the `carpobrotus_ipm` object in a stepwise fashion. However, every `define_*`

function in ipmr takes a proto_ipm as the first argument and returns a proto_ipm object. Thus, we can also use the %>% operator from the magrittr package to chain together the model creation pipeline. This example will demonstrate that process as well.

```
pred_par_list <- list(
  grow_mod = grow_mod,
  grow_sdv = grow_sd,
  surv_mod = surv_mod,
  repr_mod = repr_mod,
  flow_mod = flow_mod,
  recr_n   = recr_n,
  flow_n   = flow_n,
  recr_mu  = recr_mu,
  recr_sd  = recr_sd,
  recr_pr  = recr_pr
)

predict_method_carpobrotus <- init_ipm('simple_di_det') %>%
  define_kernel(
    name      = "P",
    formula   = S * G,
    family    = "CC",
    G         = dnorm(z_2, mu_g, grow_sdv),
    mu_g      = predict(grow_mod,
                        newdata = data.frame(log_size = z_1),
                        type = 'response'),
    S         = predict(surv_mod,
                        newdata = data.frame(log_size = z_1),
                        type = "response"),
    data_list = pred_par_list,
    states    = list(c('z')),
    evict_cor = TRUE,
    evict_fun = truncated_distributions("norm", "G")
  ) %>%
  define_kernel(
    name      = "F",
    formula   = recr_pr * f_s * f_d * p_f,
    family    = "CC",
    f_s       = predict(flow_mod,
                        newdata = data.frame(log_size = z_1),
                        type = "response"),
    f_d       = dnorm(z_2, recr_mu, recr_sd),
    p_f       = predict(repr_mod,
                        newdata = data.frame(log_size = z_1),
                        type = "response"),
    data_list = pred_par_list,
    states    = list(c("z")),
    evict_cor = TRUE,
    evict_fun = truncated_distributions("norm", "f_d")
  ) %>%
  define_k(
    name      = "K",
    family    = "IPM",
    K         = P + F,
```

```
    n_z_t_1  = K %*% n_z_t,
    data_list = list(),
    states    = list(c('z')),
    evict_cor = FALSE
  ) %>%
  define_impl(
    make_impl_args_list(
      kernel_names = c("K", "P", "F"),
      int_rule     = rep('midpoint', 3),
      dom_start    = rep('z', 3),
      dom_end      = rep('z', 3)
    )
  ) %>%
  define_domains(
    z = c(L, U, n_mesh_p)
  )  %>%
  define_pop_state(
    n_z = rep(1/100, n_mesh_p)
  ) %>%
  make_ipm(iterate    = TRUE,
           iterations = 100)
```

Further analyses

Many research questions require a bit more than just computing asymptotic growth rate (λ). Below, we will compute the kernel sensitivity, elasticity, R_0, and generation time. First, we will define a couple helper functions. These are not included in `ipmr`, but will eventually be implemented in a separate package that can handle the various classes that `ipmr` works with.

The first is sensitivity of λ to perturbations in the projection kernel. Here, we can use the `right_ev` and `left_ev` functions in `ipmr` to get the right and left eigenvectors, and then compute the sensitivity surface. Note that we have a second argument here named `d_z`. This is the width of the integration bins. We'll see how to get that from our IPM below.

```
sens <- function(ipm_obj, d_z) {

  w <- right_ev(ipm_obj)$z_w
  v <- left_ev(ipm_obj)$z_v

  return(
    outer(v, w) / sum(v * w * d_z)
  )

}
```

Next, we can define a function to compute the elasticity λ to kernel perturbations. This uses the `sens` function from above, and the `lambda()` function from `ipmr`.

```
elas <- function(ipm_obj, d_z) {

  K           <- ipm_obj$iterators$K

  sensitivity <- sens(ipm_obj, d_z)
```

```
  lamb        <- lambda(ipm_obj, comp_method = "eigen")

  out         <- sensitivity * (K / d_z) / lamb

  return(out)

}
```

We may also want to compute the per-generation population growth rate. The function below uses the sub-kernels contained in the `carpobrotus_ipm` object to do that.

```
R_nought <- function(ipm_obj) {

  Pm <- ipm_obj$sub_kernels$P
  Fm <- ipm_obj$sub_kernels$F

  I  <- diag(dim(Pm)[1])

  N  <- solve(I - Pm)

  R  <- Fm %*% N

  return(
    Re(eigen(R)$values)[1]
  )

}
```

Finally, generation time is a useful metric in many analyses. Below, we make use of our `R_nought` function with to compute one version of this quantity (though other definitions exist. Covering those is beyond the scope of this case study).

```
gen_time <- function(ipm_obj) {

  lamb     <- unname(lambda(ipm_obj, comp_method = "eigen"))

  r_nought <- R_nought(ipm_obj)

  return(log(r_nought) / log(lamb))
}
```

We need to extract the `d_z` value and meshpoints from the IPM we built. We can extract this information in a list form using the `int_mesh()` function from `ipmr` on our IPM object. The `d_z` in this case will be called `d_z` because we named our domain `"z"` when we implemented the model. However, it will have a different name if the `states` argument in `define_k(ernel)` has different different values. Once we have that, we can begin computing the life history traits of interest.

```
mesh_info <- int_mesh(carpobrotus_ipm)

sens_mat <- sens(carpobrotus_ipm, mesh_info$d_z)
elas_mat <- elas(carpobrotus_ipm, mesh_info$d_z)

R0    <- R_nought(carpobrotus_ipm)
gen_T <- gen_time(carpobrotus_ipm)

R0
```

```
## [1] 0.5079748
```

```
gen_T
```

```
## [1] 27.79469
```

We may want to visualize the results of our sensitivity and elasticity analyses. We'll go through two options: one using the `graphics` package and one using the `ggplot2` package. The `ggplot2` method will require us to define a function that transforms our matrix into a `data.frame` with 3 columns. The first two columns contain matrix indices, and the third column contains the actual values.

First, the `graphics` package.

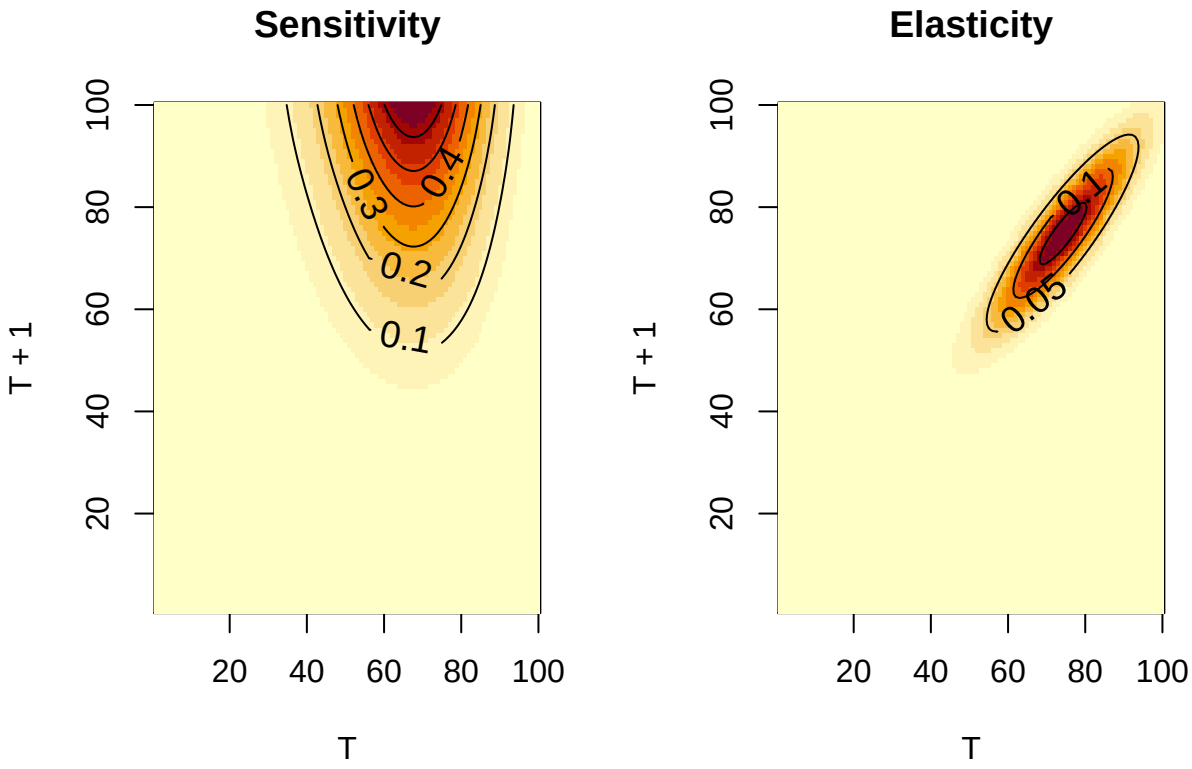
```
par(mfrow = c(1, 2))

x <- y <- seq_len(ncol(sens_mat))

image(x = x,
      y = y,
      z = t(sens_mat),
      main = "Sensitivity", xlab = "T", ylab = "T + 1")

contour(x = x,
        y = y,
        t(sens_mat),
        nlevels = 5,
        labcex = 1.2,
        add = TRUE)

image(x = x,
      y = y,
      z = t(elas_mat),
      main = "Elasticity", xlab = "T", ylab = "T + 1",
      add = FALSE)
contour(x = x,
        y = y,
        t(elas_mat),
        nlevels = 5,
        labcex = 1.2,
        add = TRUE)
```



Now, for the ggplot2 version. First, create a function to create long format data frames for each matrix. Then, get the meshpoints for the model out of the main_env. Once we have those, we can use geom_tile and geom_contour to generate the ggplots, and grid.arrange from the gridExtra package to put them side by side.

```
library(ggplot2)
library(gridExtra)

mat_to_df <- function(mat, meshp) {

  meshp$value <- NA_real_

  it <- 1

  for(i in seq_len(dim(mat)[1])) {
    for(j in seq_len(dim(mat)[2])) {

      meshp[it, 3] <- mat[i, j]
      it <- it + 1

    }
  }

  return(meshp)
}

mesh_p <- data.frame(x = mesh_info$z_1,
```

```
                    y = mesh_info$z_2)

sens_df <- mat_to_df(sens_mat, mesh_p)
elas_df <- mat_to_df(elas_mat, mesh_p)

# Create a default theme for our plots

def_theme <- theme(
  panel.background = element_blank(),
  axis.text        = element_blank(),
  axis.title.x     = element_text(
    size   = 16,
    margin = margin(
      t = 20,
      r = 0,
      l = 0,
      b = 2
    )
  ),
  axis.title.y = element_text(
    size   = 16,
    margin = margin(
      t = 0,
      r = 20,
      l = 2,
      b = 0
    )
  ),
  axis.ticks   = element_blank(),
  legend.title = element_text(size = 16)
)

sens_plt <- ggplot(sens_df) +
  geom_tile(aes(x    = x,
                y    = y,
                fill = value)) +
  geom_contour(aes(x = x,
                   y = y,
                   z = value),
               color = "black",
               size = 0.7) +
  scale_fill_gradient("Value",
                      low = "red",
                      high = "yellow") +
  scale_x_continuous(name = "T") +
  scale_y_continuous(name = "T + 1") +
  def_theme +
  ggtitle("Sensitivity")

elas_plt <- ggplot(elas_df) +
  geom_tile(aes(x    = x,
                y    = y,
                fill = value)) +
```

```
  geom_contour(aes(x = x,
                   y = y,
                   z = value),
               color = "black",
               size = 0.7) +
  scale_fill_gradient("Value",
                      low = "red",
                      high = "yellow") +
  scale_x_continuous(name = "T") +
  scale_y_continuous(name = "T + 1") +
  def_theme +
  ggtitle("Elasticity")

grid.arrange(sens_plt, elas_plt,
             layout_matrix = matrix(c(1, 2,
                                      1, 2),
                                    nrow = 2,
                                    byrow = TRUE))
```