

BIOL 7800 Semester Project: Final Report

Reproducing Montaña-Centellas et al., 2020

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1 Background

2 Ecologists have long been fascinated by patterns of biodiversity along environmental gradients
3 and the mechanisms driving these patterns (Ricklefs 2004). Elevational gradients are inter-
4 esting from this perspective, due to their rapid turnover of environmental conditions creating
5 complex sets of habitats and climate zones (Graham et al. 2014). As for how communities
6 of organisms are assembled with particular species, the two main factors generally believed to
7 play a role are environmental filtering and biotic interactions (Cavender-Bares et al. 2009).

8 These two scenarios are typically reflected in under- or overdispersion respectively in the func-
9 tional and phylogenetic structure of communities—in other words, species assemblages are
10 more clustered or dispersed in their function or phylogeny than expected by chance (Lebrija-
11 Trejos et al. 2010; Mayfield and Levine 2010). For instance, communities under strong en-
12 vironmental filtering pressure due to factors such as habitat quality and structure, resource
13 availability, or abiotic stresses like temperature typically contain species with high functional

14 similarity (Presley et al. 2018). Similarly, communities characterised by strong interspecific
15 competition, usually resulting in competitive exclusion or character displacement, likely show
16 overdispersion in species function (MacArthur and Levins 1967).

17 As a result, considering the functional and phylogenetic structure of communities can provide
18 insight into the relative importance of these drivers of community assembly (Webb et al. 2002;
19 Cavender-Bares et al. 2009). However, these aspects of diversity have historically received
20 much less attention than taxonomic diversity. Research on elevational patterns of taxonomic
21 diversity have found two main patterns (though these can be subdivided into finer patterns,
22 McCain 2009): species richness either decreases with elevation (e.g., Jankowski et al. 2013;
23 Sam et al. 2019) or peaks at mid-elevations (e.g., Toko et al. 2023).

24 The limited number of studies focusing on functional and phylogenetic diversity have found
25 decreasing trends (e.g., Hanz et al. 2019), with overdispersion at lower elevations and underdis-
26 persion at higher elevations (Hanz et al. 2019). However, most of these studies have dealt with
27 single mountains, leaving much still unknown about the generality of these patterns and their
28 deterministic strengths. This is exactly what Montaña-Centellas et al. (2020) investigated, by
29 analysing a large dataset of resident birds of 46 mountains across the globe.

30 **Process**

31 The process of obtaining the data for this (re)analysis was challenging because the authors
32 have not provided the raw datasets, but also simple at the same time because the processed

dataset has been made available on [Dryad](#). I simply downloaded the single data file and stored it in my repository at `data/montano_dryad_data.xlsx`. This file contains functional and phylogenetic richness and diversity metrics calculated at the level of 100 m elevation bands across 46 mountains of the world, along with their SESs and corresponding p-values.

Of the three main results from the paper I wanted to reproduce, I was not be able to reproduce the final analysis of the effect of latitude on patterns of elevational change, because latitude information is missing from the archived dataset¹.

The first analysis lacked clarity on the process after running quadratic regressions for the functional and phylogenetic diversity metrics against elevation. The authors mention “classifying” each elevational pattern using slope and intercept values from the model results, without mentioning specific details, and they do not provide code for this either, which suggests that they manually classified the trends. Instead, I tried to achieve the same results with a programmatic approach, using a series of hierarchical `case_when()` conditions. For the second analysis, since we do not have access to the original trait and phylogeny data, I was limited to using SES values that the authors have already calculated for each metric (with the assumption of reproducibility and absence of errors in the intermediate steps).

I used the following packages in my reproduction process: `dplyr` (Wickham et al. 2023), `tidyr` (Wickham et al. 2024), `purrr` (Wickham and Henry 2023), `readxl` (Wickham and Bryan 2023), `glue` (Hester and Bryan 2024), `stringr` (Wickham 2023), `stats` (R Core Team 2025), `lme4` (Bates et al. 2015), `broom` (Robinson et al. 2024), `broom.mixed` (Bolker and

¹Table S1.1 in the online supplementary material [PDF](#) does contain absolute latitude and longitude, but due to time constraints I was unable to import this data and run the final analysis.

53 Robinson 2024), `ggplot2` (Wickham 2016), `ggExtra` (Attali and Baker 2023), and `patchwork`
54 (Pedersen 2024). The `metafor` package (Viechtbauer 2010)—which the authors used to run
55 hierarchical multivariate meta-regression to assess latitudinal effects on deterministic signal—
56 was new to me, although I ended up not performing this analysis.

57 **Reproducible research code**

58 The below code sets up everything required to run the analyses:

```
library(dplyr)

library(tidyr)

library(stringr)

library(readxl) # file is .xlsx

library(glue)

library(ggplot2); theme_set(theme_classic())

library(ggExtra) # for marginal distribution histograms (Fig 3)

library(patchwork) # combine individual panels in Fig 3

library(purrr)

library(broom) # to easily access p-value from model objects

library(broom.mixed) # for mixed models

library(lme4)
```

```

# colour palette to match that used in paper

scale_col_pal <- scale_color_brewer(palette = "Dark2", na.value = "grey50")
scale_fill_pal <- scale_fill_brewer(palette = "Dark2", na.value = "grey50")


# load helper functions

source("sem-project/functions.R")


data_dryad <- read_xlsx("data/montano_dryad_data.xlsx",
                        sheet = "FDPD_Supporting") %>%

# normalise elevations per mountain

group_by(Mountain) %>%

mutate(elevation_norm = norm_fn(elevation)) %>%

# just realised that's not what they actually did; they just scaled and centred on 0

mutate(elevation_scaled = scale(elevation)[,1]) %>%

ungroup()

```

59 The `functions.R` file being sourced in contains several helper functions, but because it contains
60 146 lines of code, it is not reprinted here (see [source](#) instead).

61 First, to obtain patterns of diversity metrics across elevations, I fit the polynomial model for
62 each of the four diversity metrics across all 46 mountains individually, and then extract the
63 intercept and coefficients for each and also predict responses across elevations.

```

# iterate over each mountain in the dataset:

# fit LM of each metric against linear and second-order polynomial terms of Elevation
# extract intercept and coefficients for both Elevation terms
# aggregate all these values over all mountains

list_mount <- unique(data_dryad$Mountain)

metric_cols <- c("FRic", "FDis", "PD", "MPD")

to_iter <- expand.grid(mountain = list_mount, metric = metric_cols)

quad_reg <- map2(to_iter$mountain, to_iter$metric, ~ {

  data_mount <- data_dryad %>% filter(Mountain == .x)

  model_formula <- as.formula(glue("{.y} ~ elevation + I(elevation^2)"))

  model_mount <- lm(model_formula, data_mount)

  # predict only for elevations present in each mountain

  to_pred <- data_mount %>% distinct(Mountain, elevation)

  # predict

  model_pred <- predict(model_mount, newdata = to_pred, type = "response")

  pred <- bind_cols(to_pred, pred = model_pred)

```

```

# store p-value of model fit

p <- broom::glance(model_mount) %>% pull(p.value)

t(model_mount$coefficients) %>%

  as_tibble() %>%

  magrittr::set_colnames(c("intercept", "coef_linear", "coef_poly")) %>%

  bind_cols(tibble(mountain = .x, metric = .y, pval = p)) %>%

  left_join(pred, by = c("mountain" = "Mountain"))

}) %>%

  list_rbind() %>%

  relocate(metric, mountain) # bring metric and mountain cols to the start

```

64 I then plot the predicted values before classifying the trends into the nine categories the authors
 65 used: Increasing, Decreasing, Mid Peak, Mid Valley, Low Plateau (Peak), High Plateau (Peak),
 66 Low Valley, High Valley, and NS for non-significant.

```

quad_reg %>%

  ggplot(aes(x = elevation, y = pred, col = mountain)) +

  geom_line() +

  facet_wrap(~ metric, ncol = 1, scales = "free_y", strip.position = "left") +

  labs(x = "Elevation", y = "") +

```

```
# scale_col_pal + # only makes sense to colour scheme after classifying into 8 categs
theme(panel.grid.major.x = element_line(colour = "grey", linetype = "dotted"),

      # match strip format in paper

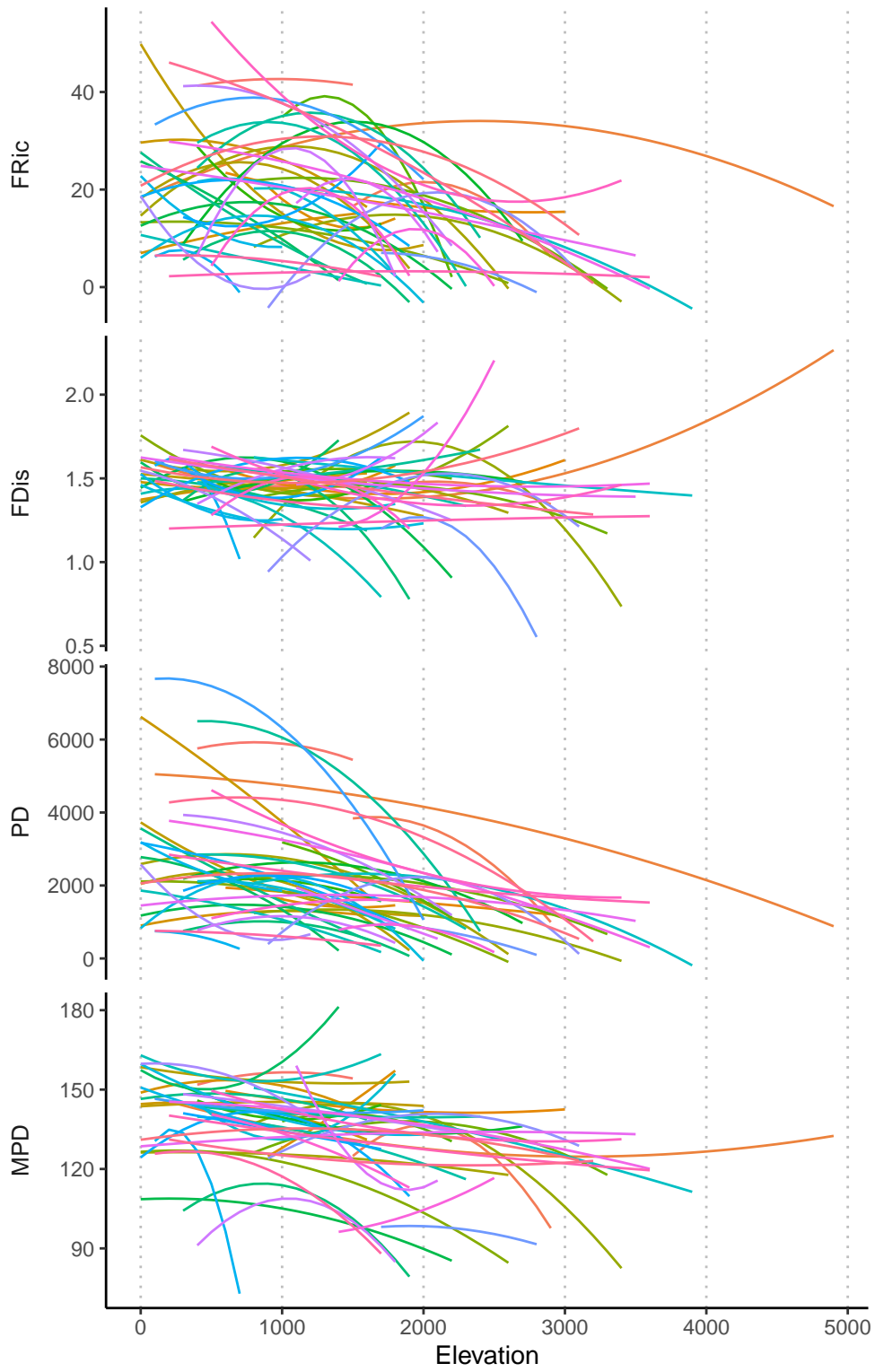
      strip.background = element_rect(colour = NA),

      strip.placement = "outside",

      strip.text = element_text(size = 10),

      # remove colour key

      legend.position = "none")
```

```

# classify elevational trends

quad_reg_class <- quad_reg %>%

  get_inflection() %>%

  get_elev_cats() %>%

  class_valley_peak() %>%

  group_by(metric, mountain) %>%

  reframe(trend = case_when(

    min(pval) > 0.1 ~ "NS",

    all(inflection == FALSE) & all(pred_diff >= 0) ~ "Increasing",
    all(inflection == FALSE) & all(pred_diff <= 0) ~ "Decreasing",

    all(valleypeak == "valley") &

      all(!(inflection == TRUE & elev_cat != "LOW")) ~ "Low Valley",
    all(valleypeak == "valley") &

      all(!(inflection == TRUE & elev_cat != "HIGH")) ~ "High Valley",
    all(valleypeak == "valley") &

      all(!(inflection == TRUE & elev_cat != "MID")) ~ "Mid Valley",

    all(valleypeak == "peak") &

```

```

    all(!(inflection == TRUE & elev_cat != "LOW")) ~ "Low Peak",

    all(valleypeak == "peak") &

    all(!(inflection == TRUE & elev_cat != "HIGH")) ~ "High Peak",

    all(valleypeak == "peak") &

    all(!(inflection == TRUE & elev_cat != "MID")) ~ "Mid Peak",

    TRUE ~ NA

  ))

# plot frequency bar graph of different trend types
quad_reg_class %>%

  mutate(trend = factor(

    trend,

    levels = c("Increasing", "Decreasing", "Mid Peak", "Mid Valley",

               "Low Peak", "Low Valley", "High Peak", "High Valley", "NS")

  )) %>%

  group_by(metric) %>%

  count(trend) %>%

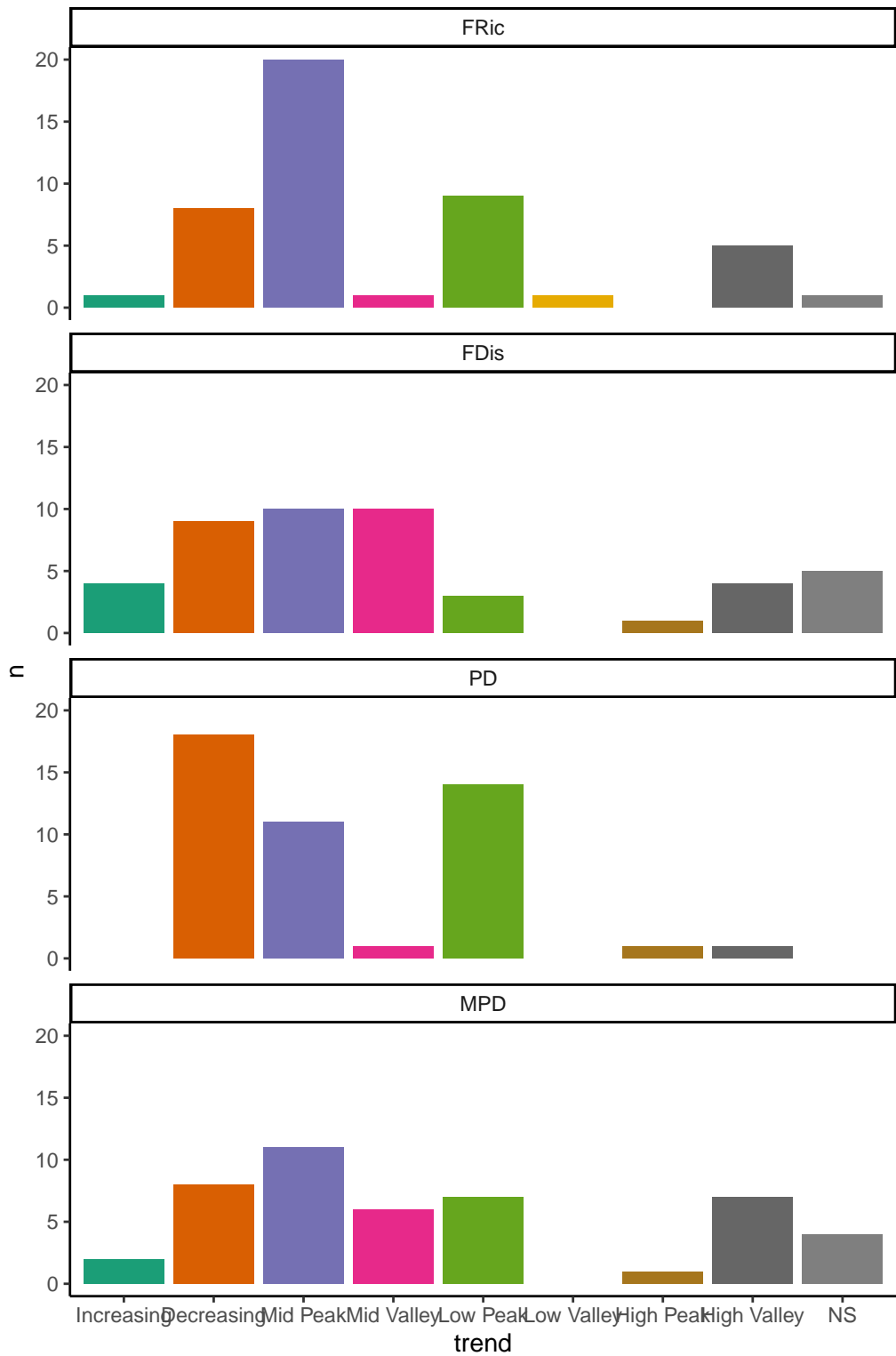
  ggplot() +

  geom_col(aes(x = trend, y = n, fill = trend)) +

  facet_wrap(~ metric, ncol = 1) +

```

```
scale_fill_pal +  
theme(legend.position = "none")
```



69 For the analysis of deterministic strength in elevational patterns, I start with the calculated
70 SES values, and fit individual linear models for each mountain separately (similar to the first
71 analysis but elevation is scaled here).

```
# iterate over each mountain in the dataset:

# fit LM of each metric against linear & 2nd-order polynomial terms of scaled elevation

# extract model predictions for each mountain

metric_sess <- glue("SES.{metric_cols}")

to_iter <- expand.grid(mountain = list_mountain, metric = metric_sess)

quad_reg_ses <- map2(to_iter$mountain, to_iter$metric, ~ {

  data_mountain <- data_dryad %>% filter(Mountain == .x)

  model_formula <- as.formula(glue("{.y} ~ elevation_scaled + I(elevation_scaled^2)"))

  model_mountain <- lm(model_formula, data_mountain)

  # predict only for elevations present in each mountain

  to_pred <- data_mountain %>% distinct(Mountain, elevation_scaled)

  # predict

  model_pred <- predict(model_mountain, newdata = to_pred, type = "response")

  pred <- bind_cols(to_pred, pred = model_pred)
```

```

tibble(mountain = .x, metric = .y) %>%

  left_join(pred, by = c("mountain" = "Mountain"))

}) %>%

list_rbind() %>%

relocate(metric, mountain) %>% # bring metric and mountain cols to the start

mutate(metric = gsub("\\\\.", " ", metric)) %>% # remove period from metric name

mutate(metric = factor(metric,

                        levels = c("SES FRic", "SES FDis", "SES PD", "SES MPD")))

# summarise original data to plot raw data points

data_dryad_ses <- data_dryad %>%

  select(Mountain, elevation_scaled, starts_with("SES")) %>%

  pivot_longer(cols = starts_with("SES"),

               names_to = "metric", values_to = "obs") %>%

  rename(mountain = Mountain) %>%

  mutate(metric = gsub("\\\\.", " ", metric)) %>% # remove period from metric name

  mutate(metric = factor(metric,

                        levels = c("SES FRic", "SES FDis", "SES PD", "SES MPD")))

```

72 Then, I fit the linear mixed-effects model testing the diversity metrics as a function of scaled
73 elevation. This time, I extract not only model predictions, but also the model summary to
74 prepare Table 1.

```
quad_lmm_ses_output <- map(metric_ses, ~ {  
  
  model_formula <- as.formula(glue(  
    "{.x} ~ elevation_scaled + I(elevation_scaled^2) + (1 | Mountain)"  
  ))  
  
  # REML = FALSE because we use Likelihood Ratio Test  
  
  model_ses <- lmer(model_formula, data_dryad, REML = FALSE)  
  
  # predict only for elevations present in each mountain  
  
  to_pred <- data_dryad %>% distinct(elevation_scaled)  
  
  # predict  
  
  model_pred <- predict(model_ses, newdata = to_pred, type = "response",  
    re.form = NA)  
  
  pred <- bind_cols(to_pred, pred = model_pred) %>% mutate(metric = .x)  
  
  # also generate model summary for Table 1  
  
  summ <- gen_mem_summ(model_ses) %>% mutate(metric = .x)
```



```

# return both

list(predicted = pred,

      summary = summ)

})

# model predictions

quad_lmm_ses <- map(quad_lmm_ses_output, "predicted") %>%

  list_rbind() %>%

  relocate(metric) %>% # bring metric col to the start

  mutate(metric = gsub("\\.", " ", metric)) %>% # remove period from metric name

  mutate(metric = factor(metric,

                          levels = c("SES FRic", "SES FDis", "SES PD", "SES MPD")))

# model summary

quad_lmm_ses_summ <- map(quad_lmm_ses_output, "summary") %>%

  list_rbind() %>%

  relocate(metric) %>%

  # refining formatting of labels and values

  mutate(metric = gsub("\\.", " ", metric), # remove period from metric name

         term = str_replace(term, "elevation_scaled", "Elevation")) %>%

```

```

mutate(term = if_else(str_detect(term, "\\("),
                        str_match(term, "\\(([^()]*\\)")[, 2],
                        term) %>%
                        str_replace_all("\\^2", "<sup>2</sup>")) %>%
mutate(term = str_replace(term, "Mountain", "Mountain (random effect)")) %>%
pivot_wider(names_from = "metric", values_from = "value") %>%
rename(Terms = term)

```

75 Finally, Figure 3 of the original paper is created as a **patchwork** as opposed to simple facetting,
 76 due to the complicated nature of each panel (specifically, the marginal histograms), and the
 77 model summary extracted above is depicted as a table.

```

fig3_panel <- function(which_metric) {

  (

    # base plot

    ggplot() +

      # raw data points

      geom_point(data = data_dryad_ses %>% filter(metric == which_metric),
                  col = "grey", alpha = 0.5,
                  mapping = aes(x = elevation_scaled, y = obs, group = mountain)) +

      # individual mountain model predictions (blue line)

```

```

    geom_line(data = quad_reg_ses %>% filter(metric == which_metric),
              col = "#00538F",
              mapping = aes(x = elevation_scaled, y = pred, group = mountain)) +
    geom_hline(yintercept = 0) +
    # overall LMM prediction across all mountains (black line)
    geom_line(data = quad_lmm_ses %>% filter(metric == which_metric),
              linewidth = 1.25,
              mapping = aes(x = elevation_scaled, y = pred)) +
    labs(x = "Elevation (scaled)", y = which_metric) +
    # match strip format in paper
    theme(axis.title.y = element_text(size = 10))
  ) %>%
  # include marginal histograms
  ggMarginal(type = "histogram", fill = "grey")
}

metric_sess_form <- gsub("\\\\.", " ", metric_sess)

(wrap_elements(fig3_panel(metric_sess_form[1])) |
  wrap_elements(fig3_panel(metric_sess_form[2]))) /

```

```
(wrap_elements(fig3_panel(metric_sess_form[3]))) |  
  
  wrap_elements(fig3_panel(metric_sess_form[4]))) &  
  
plot_annotation(tag_levels = "a", tag_prefix = "(", tag_suffix = ")") &  
  
theme(plot.tag.position = c(0.05, 0.95)) # align tags with axis labels
```

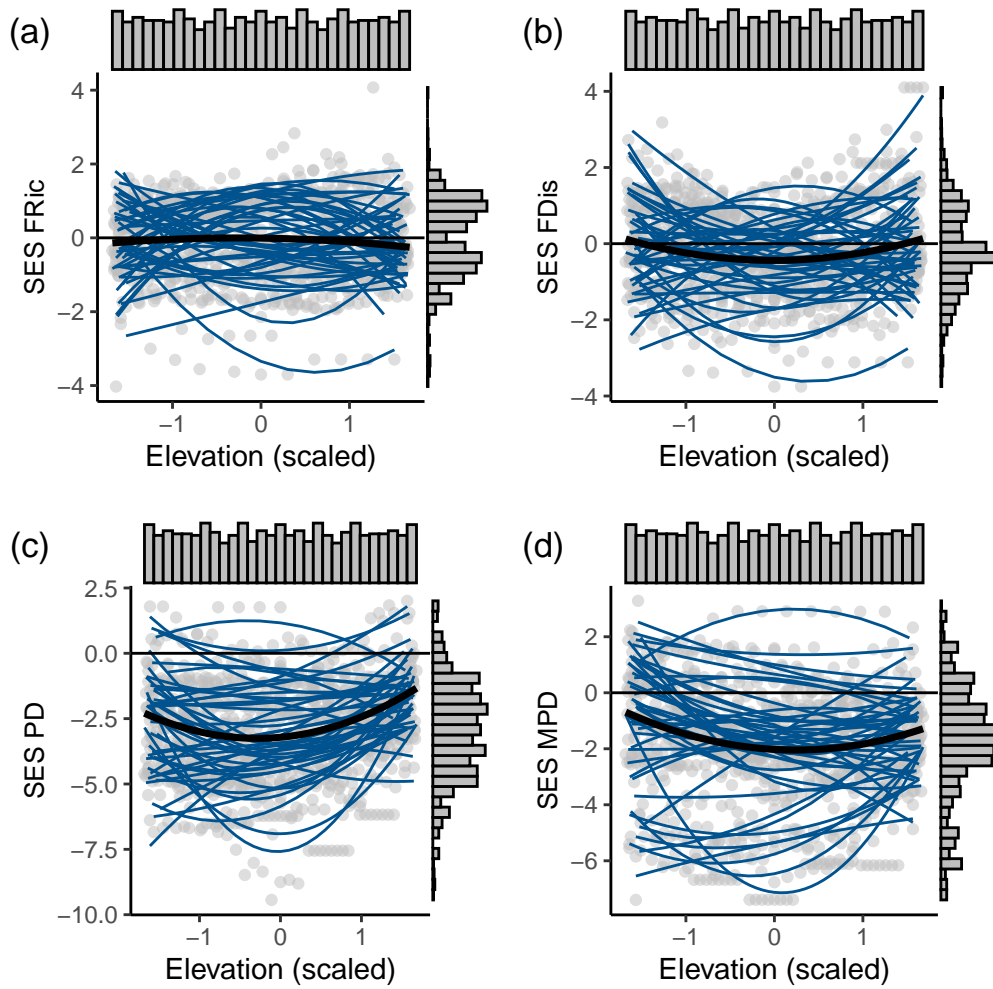


Table 1: Parameter estimates (with SE) of mixed-effects models. The last row shows variances of the random effect term, Mountain.

Terms	SES FRic	SES FDis	SES PD	SES MPD
Intercept	-0.007 ± 0.111	-0.439 ± 0.118	-3.212 ± 0.222	-2.023 ± 0.268
Elevation	-0.035 ± 0.028	0.004 ± 0.03	0.285 ± 0.036**	-0.177 ± 0.034**
Elevation2	-0.067 ± 0.032*	0.2 ± 0.034**	0.496 ± 0.041**	0.367 ± 0.039**
Mountain (random effect)	0.487	0.541	2.135	3.192

79 Learnings and takeaways

80 I would not say that any one aspect of the exercise was particularly most instructive, but go-
81 ing through this process and realising that my reproduction still contains gaps despite getting
82 the same final results, has reaffirmed to me how difficult it is to achieve 100% reproducibility
83 especially when not following a code-first approach. By this I mean a workflow which does
84 not just create code as and when the need arises, patching together the different moving parts
85 after the fact, or which does not irreparably decouple code and outputs from text (reports,
86 manuscripts); I mean a workflow that follows more of a software development approach in-

87 involving iterative optimisation, stress testing and cleaning of code; functional and modular
88 programming; version control, etc. The different tools and features provided by the tidyverse
89 and its *tidy* philosophy as well as RStudio and R Projects are designed to help with just this,
90 but still fall outside the workflows of many scientists working with R.

91 For instance, one point of confusion and frustration for me was the lack of information on
92 how the authors actually performed the classification of trends. Even if they had not done the
93 classification using code, some basic testing of the analytical pipeline would have identified
94 this particular “gap” in information. In my case, since there was no original code to begin
95 with, the reproduction process probably ended up being much less frustrating than it could
96 have been, based on my conversations with peers in the class. In most of those cases, issues
97 with the code usually traced back to some of these fundamental points outlined above.

98 All of this has made me start thinking, rather radically, that the field of ecology and evo-
99 lutionary biology as a whole should start placing greater and stricter emphasis on coding
100 practices instead of simply focusing on learning a particular programming language. Courses
101 such as this current one should be mandated for students entering research careers. Journals
102 should introduce strict code-related acceptance criteria and also enforce them (which we have
103 seen does not happen as much), specifically avoiding publishing studies whose codebases are
104 not immediately or relatively quickly reproducible. For long, I have remained fundamentally
105 against mandates and coercion, acknowledging the significant costs associated with learning
106 and adopting these tools and approaches. However, just like ecologists quickly accepted the
107 notoriously steep learning curves of R and Python as nothing but a rite of passage, just like

108 universities and institutions quickly (and questionably) accepted the ridiculous dollar costs of
109 open-access publishing, just like authors have learned that there is a net positive to mandatory
110 open data archiving—sometimes we just need a paradigm shift and that is okay.

111 I have been improving my personal workflow for a few years now, and I think I am currently
112 in a decent place. But as an example of applying some of my learnings from this project into
113 my own research, I think I will be selective about not just the journals I submit my own work
114 to (e.g., avoid journals with page limits on supplementary material), but also the journals
115 I choose to review for (e.g., how are their data and code archiving policies?). Additionally,
116 I will choose not to review manuscripts that do not have reasonably “good” codebases. My
117 [response to the ethos question in Activity 2](#) has not really changed, but there I had highlighted
118 the non-negligible costs involved in all this; in order to lower these costs and to help people
119 transition to open and reproducible workflows and approaches, I want to create or curate some
120 resources *in an effective manner*. For example, I will create a slide deck (perhaps interactive)
121 to use in a walkthrough-like presentation to my labmates, which will highlight certain practical
122 aspects like live and remote collaboration, or version control, without diving into technical or
123 theoretical nitty-gritties.

124 Lastly, I will also be reflecting more over the coming weeks, and I hope to finally articulate
125 my personal manifesto for reproducible and open research, and publish it on my website.

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